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The Mollusk Assemblage Associated with Fronds of Giant Kelp (*Macrocystis pyrifera*) off Santa Catalina Island, California

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Abstract.—The mollusk assemblage associated with giant kelp (*Macrocystis pyrifera*) fronds off Santa Catalina Island, California was examined monthly from June 1975 through December 1976. Mollusks comprised 1.0, 1.6, and 2.9% (by number) of all invertebrates associated with kelp fronds in the canopy, middle, and bottom zones of the kelp forest, respectively. Forty one species (36 gastropods, 5 bivalves) were collected, ranging from 14–28 for any given month. The mean number of species present was greater in the bottom (16.9) and middle zones (15.6) than in the canopy (9.3). Most species (29) were rare in occurrence (<1/kg kelp) and small (<4 mm) in size. Throughout the study, more mollusks were found in the bottom zone than in the middle; fewest numbers were present in the canopy. Most species reflected this general pattern; only the nudibranch *Polycera tricolor* was more abundant in the canopy than in the lower zones. As a group, mollusks were most abundant on *Macrocystis* fronds during summer–fall.

Mollusks are an important group of invertebrates within giant kelp forests (*Macrocystis pyrifera*) along the coast of California. Several species are herbivores and utilize the kelp as food (Jones 1971; Leighton, 1971; Rosenthal et al. 1974), whereas others serve as a food resource for invertebrates and fishes residing within the kelp forests (Quast 1968; Feder et al. 1974; Hobson and Chess 1976; Schmitt 1982; Schmitt et al. 1983).

Little is known about the life history and distributions of most mollusks associated with the fronds of *Macrocystis,* and no studies have examined the frond-associated assemblage over extended periods of time. North (1971) and Pearse and Lowry (1974) listed the mollusks found within kelp forests off southern and northern California, respectively. Wing and Clendenning (1971) examined the motile invertebrates associated with clean and encrusted *Macrocystis* blades at three different depths during spring and summer, but did not identify individual species of mollusks. Rosenthal et al. (1974) identified invertebrate species associated with southern California kelp forests, but only two species of mollusks were chosen for intensive quantitative analysis during the seven-year study. During a six-month study, Miller and Geibel (1973) collected nine species of canopy-associated mollusks, but the sampling method collected only those individuals larger than 10 mm in length. Several studies (Lowry et al. 1974; Riedman et al. 1981; Watanabe 1984) have examined the spatial segregation of *Tegula* spp. and/or

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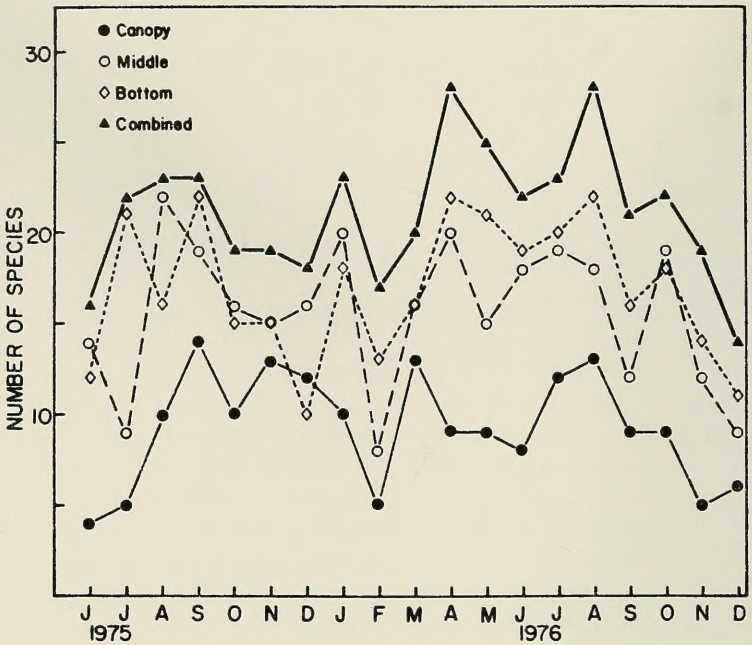

Fig. 1. The number of mollusk species present in each of the vertical zones. Many species are present in more than one zone. Grand means ($\bar{x}$ ± 95% C.I.): 9.3 ± 1.5 (Canopy), 15.6 ± 2.0 (Middle), 16.9 ± 1.9 (Bottom).

Calliostoma spp. within central California kelp forests, but other mollusks were not studied.

The present report examines the spatial distribution, abundance, and seasonal dynamics of all mollusks associated with the fronds of giant kelp at Santa Catalina Island (California) over a 19-month period. A general overview of the entire assemblage and a detailed examination of the most abundant species are presented.

Materials and Methods

The study was conducted at Habitat Reef, located in Big Fisherman Cove, Santa Catalina Island, California, USA (33°28′N, 118°20′W). Habitat Reef is a 100-m underwater extension of the lava-breccia cliffs which form the south headland of the cove. Beginning at the cliff base, the reef slopes gently to a depth of 18 m, then becomes steeper and terminates at a depth of 25 m. The substrate of the shallow portion (<3 m depth) was covered by a rich algal-invertebrate turf, whereas the deeper portion (>3 m depth) was dominated by giant kelp and had very little understory algae.

Monthly samples were collected from giant kelp plants in the central portion of the Habitat Reef kelp forest (7–9 m depth) during tidal heights from +1.0 to +1.3 m MLLW. I divided the kelp forest at Habitat Reef into three vertical zones: the canopy (water surface to a depth of 1 m), bottom (just above the holdfasts to 2 m above the substrate), and middle (area between the canopy and bottom). Holdfasts were not examined. Three replicate samples were collected from each zone from June through September 1975; five replicates were collected from October 1975 through December 1976. Only one sample was collected from any

Table 1. Mean abundance ($\bar{\#}$/kg kelp) of all species of mollusks within each depth zone. All values are averaged over the entire 19 month study. Parenthetical values are size ranges in mm; all specimens were preserved before measuring. Abundances $\ll 0.1$ indicate that 1–3 specimens were collected during the entire study.

Species	Canopy	Middle	Bottom
Gastropoda			
Prosobranchia			
Archeogastropoda			
Tricolia pulloides (Carpenter, 1865) (0.7–1.6)	0.2	3.5	26.1
Tricolia rubrilineata (Strong, 1928) (0.7–1.4)	<0.1	<0.1	0.1
Norrisia norrisi (Sowerby, 1838) (4.0–49.0)	<0.1	0.2	0.2
Tegula aureotincta (Forbes, 1852) (15.0–26.0)	<0.1	0.1	<0.1
Haliotis sp. (1.5–1.6)	0	0	<0.1
Mesogastropoda			
Crepidula sp. (0.7–3.2)	7.1	28.0	79.6
Barleeia californica Bartsch, 1920 (0.6–2.0)	0.2	3.7	10.1
Amphithalamus inclusus Carpenter, 1864 (0.5–1.2)	<0.1	1.0	6.0
Amphithalamus tenuis Bartsch, 1911 (1.0–1.2)	<0.1	0.9	4.4
Lacuna unifasciata Carpenter, 1857 (0.8–5.4)	0.5	0.6	0.2
Merelina aequisculpta (Keep, 1887) (1.0–1.6)	<0.1	0.1	0.1
Rissoina sp. (1.0–1.1)	≪0.1	<0.1	<0.1
Caecum californicum Dall, 1885 (1.4–2.6)	0	<0.1	<0.1
Fartulum occidentale (Dall, 1885) (1.5–1.6)	0	≪0.1	<0.1
Cerithiopsis sp. (0.6–3.2)	0	0	<0.1
Balcis thersites (Carpenter, 1864) (1.4–1.5)	0	0	<0.1
Bittium sp. (6.6)	0	≪0.1	0
Neogastropoda			
Granulina margaritula (Carpenter, 1857) (0.6–2.1)	4.6	52.6	32.9
Mitrella tuberosa (Carpenter, 1864) (1.4–7.1)	1.1	2.3	1.1
Amphissa sp. (1.0–2.4)	0	0.5	0.8
Mitrella carinata (Hinds, 1844) (6.7–7.2)	0.1	<0.1	0.2
Conus californicus Reeve, 1844 (1.5–1.8)	0	<0.1	≪0.1
Opistobranchia			
Cephalaspidea			
Aglaja inermis (Cooper, 1862) (2.0–5.0)	0.2	0.9	0.3
Nudibranchia			
Polycera tricolor Robilliard, 1971, (2.7–8.0)	8.5	5.6	1.1
Melibe leonina (Gould, 1852) (3.4–9.4)	1.1	2.1	2.9
Hermissenda crassicornis (Eschscholtz, 1831) (2.4–6.4)	<0.1	1.3	3.0
Eubranchus rustyus (Marcus, 1961) (1.5–3.4)	0.1	3.4	1.1
Corambe pacifica MacFarland and O'Donoghue, 1929 (1.0–2.2)	<0.1	0.3	<0.1
Antiopella barbarensis (Cooper, 1863) (3.6–11.4)	<0.1	0.1	0.2
Dendronotus frondosus (Ascanius, 1774) (1.9–9.6)	<0.1	0.1	0.2
Flabellinopsis iodinea (Cooper, 1862) (2.8–6.2)	0	0.1	<0.1
Coryphella pricei MacFarland, 1966 (5.0–6.0)	0	≪0.1	0
Pyramidella			
Odostomia sp. A. (0.5–1.8)	0.1	1.7	1.8
O. navisa Dall & Bartsch, 1909 (1.7–1.8)	0	<0.1	<0.1
O. virginalis Dall & Bartsch, 1903 (0.6–1.8)	0	0	<0.1
O. sp. B. (2.3)	≪0.1	0	0

Table 1. Continued.

Species	Canopy	Middle	Bottom
Bivalvia			
Pteriomorpha			
Arcoida			
Philobrya setosa (Carpenter, 1864) (1.3–2.3)	0	<0.1	0.1
Pterioida			
Lima sp. (1.1–1.2)	0	0	<0.1
Leptopecten sp. (2.0–9.2)	0	0	<0.1
Heterodonta			
Myoida			
Hiatella artica (Linnaeus, 1767) (0.8–2.3)	<0.1	0.8	1.0
Veneroida			
Halodakra brunnea (Dall, 1916)((0.6–1.8)	<0.1	0.6	3.0

plant. Fronds were severed at zone junctions; the middle and bottom zones were collected by carefully severing the upper zones and allowing them to drift away. Disturbance to the desired zones during this procedure was negligible. Similar amounts of kelp were collected from each zone throughout the study ($\overline{kg}$ kelp = 2.5, Canopy; 2.1, Middle; 2.3, Bottom; all n = 19).

Scuba divers collected the kelp-associated mollusks (and other invertebrates) by maneuvering a small plankton net (1 m diam, 3 m length, 0.33 mm mesh) over the desired portion of the plant, severing the fronds, and closing the net. The enclosed kelp was then placed into a large container of warm fresh water (providing a thermal and salinity shock), vigorously agitated, and removed piece by piece. The remaining water was filtered through a 0.25 mm sieve and the residue preserved. A repeat of the agitation-freshwater method four hours later indicated that 94.1, 98.9, and 98.8% (by number) of all mollusks in the canopy, middle, and bottom, respectively, were removed by the initial treatment.

Mollusks were identified (using McLean 1969) and measured using a dissecting microscope with an ocular micrometer. The wet-weight of kelp from each sample was measured, and abundances of all mollusks were expressed as the number of individuals per kg (wet-weight) of kelp. All samples are deposited at the Catalina Marine Science Center Museum.

Results

When averaged over the entire 19 month study, mollusks accounted for 1.0, 1.6, and 2.9% (by number) of all invertebrates in the canopy, middle, and bottom, respectively ($\overline{\#}$ mollusks/kg kelp $\pm$ 95% C.I.: Canopy, 25.7 $\pm$ 14.3; Middle, 111.3 $\pm$ 21.7; Bottom, 176.5 $\pm$ 47.0). Arthropods were dominant in each of the three zones, accounting for 97% of all invertebrates in the canopy, 94% in the middle, and 95% in the bottom (see Coyer, 1984). Forty-one species of mollusks (36 gastropods, 5 bivalves) were collected from all zones during the study, ranging from 14–28 for any given month (Fig. 1, Table 1). When ranked by mean monthly abundance (mean of all zones), only *Crepidula* sp. (unidentified juveniles) and *Granulina margaritula* were common (10–100/kg kelp), whereas 10 species were uncommon (1–10/kg kelp), and 29 were rare (<1/kg kelp).

Throughout the study, a greater number of species and individuals were present in each of the lower zones than in the canopy. The mean number of species (averaged over the 19 month study) in the bottom (16.9) and middle (15.6) were similar, but greater than the mean number present in the canopy (9.3; Fig. 1). The nudibranch, *Polycera tricolor,* was the most abundant species in the canopy, largely because of high numbers in October 1975, and it was the only species more abundant in the canopy than in the lower zones (Fig. 2, Table 1). For the remaining species of gastropods, 11 were more abundant in the middle, 18 more abundant in the bottom, and 6 were present equally in both zones (Table 1). Each of the five bivalves collected were absent or rare in the upper zones; three were rare and two were uncommon in the bottom.

With respect to numbers of individuals, more mollusks ($\bar{x} \pm 95\%$ C.I.) were present in the bottom zone (176.2 ± 47.0) than in the middle (111.3 ± 21.7; Fig. 3). Fewest numbers were found in the canopy (25.7 ± 14.3). The general pattern occurred throughout the study except for five months when the number of mollusks present in the middle was slightly higher than in the bottom.

Crepidula sp. and *G. margaritula* were the most abundant species during the study, collectively accounting for 45.5% (by number) of the mollusks in the canopy, 72.4% of those in the middle, and 63.7% of all mollusks in the bottom (Table 1). Five species comprised 87, 84, and 88% (by number) of all mollusks in the canopy, middle, and bottom, respectively (Table 2). With regard to overall occurrence, each of the five canopy species were uncommon (1–10/kg kelp); two and four species were common (10–100/kg kelp) in the middle and bottom, respectively.

As a group, mollusks were more abundant on *Macrocystis* fronds during summer–fall than during winter–spring (Fig. 3). Annual summer–fall peaks of abundance were suggested for *Barleeia californica* and *Tricolia pulloides,* although the latter was much more abundant in 1975 than in 1976 (Fig. 2). *Crepidula* sp. was most abundant during spring–summer 1975 then declined in numbers, whereas *G. margaritula* was present in low numbers during spring–summer 1975 then increased to maximum abundance during summer–fall 1976. No temporal patterns were evident for *P. tricolor* and abundances of all other mollusks were too low to detect any seasonal trends.

Seventy-seven percent of the shelled species (Table 1) and 78–88% of shelled individuals in each zone (Table 2) were less than 4 mm in total length. The two most abundant species, *Crepidula* sp. and *G. margaritula,* never exceeded 3.2 and 2.1 mm, respectively. *Tegula aureotincta* (15–26 mm) and *Norrisia norrisi* (4–49 mm) were by far the largest species, but both rarely were encountered.

Discussion

Several invertebrate species display patterns of horizontal and/or vertical distribution within central and southern California kelp forests, including bryozoans (Bernstein and Jung 1979), crustaceans (Hines 1982; Coyer 1984), and mollusks (Lowry et al. 1974; Riedman et al. 1981; Watanabe 1984). Frond-associated mollusks at Habitat Reef also revealed clear and consistent patterns of vertical zonation, with far more species and individuals found in the lower zones than in the canopy. Only the nudibranch, *P. tricolor,* was more abundant in the upper zones than in the bottom.

Several factors may account for the patterns of vertical zonation observed at

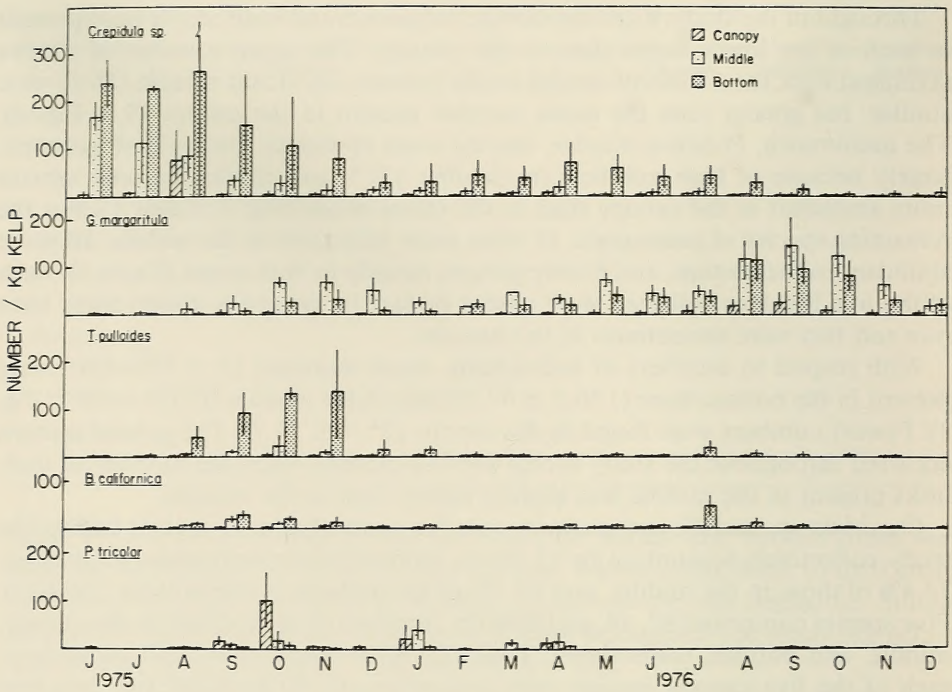

Fig. 2. Monthly abundances ($\bar{x} \pm 95\%$ C.I.) of mollusks (all species) in each vertical zone. Each value represents the mean of 3 (July–September 1975) or 5 (October 1975–December 1976) replicate samples.

Habitat Reef. The most important factor may be water motion generated by storms and/or tidal currents, which undoubtedly dislodges many mollusks from the kelp fronds. As the degree of motion and removal probably is greatest in the canopy and as all dislodged mollusks must crawl back onto the kelp via the bottom zone, the observed patterns of vertical zonation could be explained most often by differential water motion/dislodgement with subsequent concentration in the lower zones.

Other factors may be important, however, especially during extended periods of relatively calm conditions. For example, mollusks may avoid the canopy during calm summer months at Habitat Reef because of warmer surface temperatures and/or greater light intensity.

Additionally, predators may influence the vertical distribution of mollusks at Habitat Reef, although their effect is difficult to assess. Dense alga cover has been demonstrated to decrease the effectiveness of sea star predation (Watanabe 1984) as well as predation by fishes (Vince et al. 1976; Heck and Thoman 1981; Peterson 1982; Stoner 1982). Consequently, one could predict that most mollusks would be present in the bottom and canopy regions at Habitat Reef, because kelp biomass consists of a dense and "bushy" cluster of sporophytes in the bottom, a dense mass of interdigitating fronds and blades in the canopy, and a relatively sparse mass of fronds and blades in the middle. Furthermore, mollusks can avoid benthic predators by climbing up the kelp fronds where fewer predators are present (Harrold 1982; Schmitt et al. 1983; Watanabe, 1984). If reduction of predation pressure

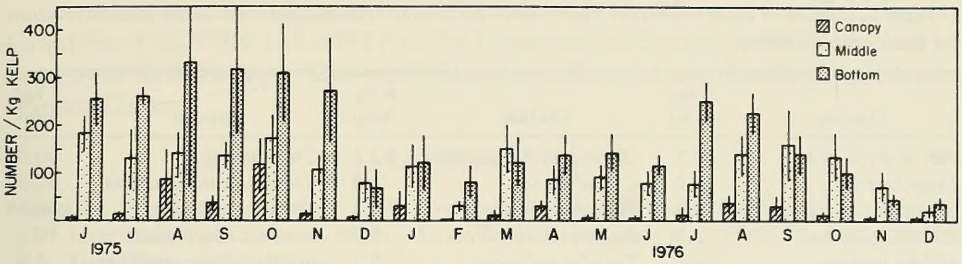

Fig. 3. Monthly abundances ($\bar{x} \pm$ 95% C.I.) of the mollusks, *Crepidula* sp., *Granulina margaritula, Tricolia pulloides, Barleeia californica,* and *Polycera tricolor* in each vertical zone. Each value represents the mean of 3 (July–September 1975) or 5 (October 1975–December 1976) replicate samples.

is an important factor in determining spatial abundance of mollusks at Habitat Reef, the number of mollusks in the canopy should be similar to numbers found in the bottom. The consistently low numbers of mollusks in the canopy, however, suggests that decreased predation pressure probably does not influence the number of mollusks in the canopy. The importance of predation in the bottom zone remains to be determined.

The majority of shelled mollusks (species and individuals) associated with fronds of giant kelp at Habitat Reef are less than 4 mm in length with only two species exceeding 10 mm. In contrast, several species of shelled gastropods associated with fronds of giant kelp in central California (Monterey) are larger than 10 mm in length (Miller and Geibel 1973; Lowry et al. 1974; Riedman et al. 1981; Watanabe 1984) and the number of individual gastropods greater than 10 mm can be substantial, especially in summer (Miller and Geibel 1973; Watanabe 1984). Although none of the larger species found at Monterey were present at Habitat Reef and all are rarely found off Santa Catalina Island (Engle, unpub. data), the difference in mollusk sizes between Monterey and Habitat Reef is intriguing and merits further investigation.

The total amount of kelp biomass is a potentially important mechanism governing the numbers of mollusks within a kelp forest. More kelp-associated mollusks (species and individuals) might be expected in a dense, rather than a sparse forest, and this pattern was observed at Habitat Reef. Kelp density was high and relatively constant (Coyer 1984) during most of the study (June 1975 through August 1976) when mollusk density also was highest. Beginning in June 1976, an anomalous warming trend associated with the El Nino of 1976–77 (for discussion of the El Nino, see Smith 1983; Rasmusson and Wallace 1983) resulted in a dramatic reduction of kelp density by September 1976 and the near disappearance of the canopy by December 1976 (Coyer 1984). Fewer mollusks were present in the much reduced canopy during the latter portion of 1976.

Without experimental data, however, it is difficult to attribute the decline in mollusk abundance solely to the decline in kelp biomass, as oceanographic conditions undoubtedly are a confounding factor. For example, the onset of warm water in mid-1976 may have reduced local larval settlement in those species exhibiting lower abundances in summer–fall 1976 than in 1975 (*Crepidula, T. pulloides, B. californica*), thereby influencing population sizes before the amount of kelp became critical. The two most abundant mollusks during the study, *Cre-*

Table 2. The five most abundant mollusks in each zone. Abundances are mean monthly values for the 19 month study.

Canopy	$\bar{\#}$ kg/ kelp	Middle	$\bar{\#}$ kg/ kelp	Bottom	$\bar{\#}$ kg/ kelp
Polycera tricolor	8.5	*Granulina margaritula*	52.6	*Crepidula* sp.	79.6
Crepidula sp.	7.1	*Crepidula* sp.	28.0	*Granulina margaritula*	32.9
Granulina margaritula	4.6	*Polycera tricolor*	5.6	*Tricolia pulloides*	26.1
Mitrella tuberosa	1.1	*Barleeia californica*	3.7	*Barleeia californica*	10.1
Melibe leonina	1.1	*Tricolia pulloides*	3.5	*Amphithalamus inclusus*	6.0

pidula sp. and *G. margaritula,* displayed non-overlapping peaks of abundance with the former most abundant during spring–summer 1975 and the latter during summer–fall 1976. The non-overlapping patterns may represent differential recruitment as a result of changing oceanographic conditions.

Little is known about the feeding biology of the most abundant mollusks associated with fronds of giant kelp at Habitat Reef, except for *Melibe leonina* which feeds on micro-crustaceans (Ajeska and Nybakken 1976) and *T. pulloides* which grazes diatoms from algal surfaces (Mooers 1982). Information from studies on congenerics, however, suggests that feeding is diverse and includes bryozoan predators (*Polycera*), micro-carnivore/detrital feeders (*Mitrella*), and filter feeders (*Crepidula*) (McDonald and Nybakken 1978; Abbott and Haderlie 1980).

Most of the mollusks associated with kelp fronds at Habitat Reef are at least present, and many are more abundant, in intertidal and subtidal non-kelp habitats along the California coast and all of the shelled gastropods are found on gravel bottoms, as well (McLean 1969; Carlton and Roth 1975; Engle 1979; Abbott and Haderlie 1980; Haderlie and Abbott 1980; Stewart and Myers 1980). Some genera such as *Haliotis, Crepidula, Amphissa,* and *Lima* are found on kelp only as juveniles (McLean, pers. comm.). In addition, several species reported to be occasionally or seasonally abundant in other giant kelp forests along the southern and central coast of California such as *Lacuna unifasciata, Mitrella carinata, N. norrisi, T. aureocinta, Leptopecten* sp. and *M. leonina* (Limbaugh 1955; Jones 1971; Pearse and Lowry 1974; Ajeska and Nybakken 1976; Bernstein and Jung 1979) were present in low numbers at Habitat Reef throughout the 19-month study. Such patterns suggest that local events and conditions strongly influence composition and dynamics of the mollusk assemblage associated with fronds of giant kelp. Additional non-kelp and giant kelp habitats need to be examined for extended periods of time before general predictions can be proposed.

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Literature Cited

Abbott, D. P., and E. C. Haderlie. 1980. Prosobranchia: Marine snails. Pp. 230–307 *in* Intertidal invertebrates of California. (R. H. Morris, D. P. Abbott, and E. C. Haderlie, eds.), Stanford Univ. Press, xiv + 690 pp.

Ajeska, R. A., and J. Nybakken. 1976. Contributions to the biology of *Melibe leonina* (Gould, 1852) (Molluska: Opistobranchia). The Veliger, 19:19–26.

Bernstein, B. B., and N. Jung. 1979. Selective pressures and coevolution in a kelp canopy community in southern California. Ecol. Monogr., 49:335–355.

Carlton, J. T., and B. Roth. 1975. Phylum Molluska: shelled gastropods. Pp. 467–514 *in* Lights manual, intertidal invertebrates of the central California coast, 3rd Ed. (R. I. Smith and J. T. Carlton, eds.), Univ. California Press, xvii + 716 pp.

Coyer, J. A. 1984. The invertebrate assemblage associated with the giant kelp *Macrocystis pyrifera,* at Santa Catalina Island, California: a general description with emphasis on amphipods, copepods, mysids, and shrimps. Fish. Bull., U.S., 82:55–66.

Engle, J. M. 1979. Ecology and growth of juvenile California spiny lobster, *Panulirus interruptus* (Randall). Ph.D. Thesis, Univ. Southern Calif., 289 pp.

Feder, H. M., C. H. Turner, and C. Limbaugh. 1974. Observations of fishes associated with kelp beds in southern California. Calif. Dept. Fish and Game, Fish Bull., 160:1–144.

Haderlie, E. C., and D. P. Abbott. 1980. Bivalvia: the clams and allies. Pp. 355–411 *in* Intertidal invertebrates of California. (R. H. Morris, D. P. Abbott, and E. C. Haderlie, eds.), Stanford Univ. Press, xiv + 690 pp.

Harrold, C. 1982. Escape responses and prey availability in a kelp forest predator-prey system. Amer. Nat., 119:132–135.

Heck, K. L., Jr., and T. A. Thoman. 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. J. Exp. Mar. Biol. Ecol., 53:125–134.

Hines, A. H. 1982. Coexistence in a kelp forest: size, population dynamics, and resource partitioning in a guild of spider crabs (Brachyura, Majidae). Ecol. Monogr., 52:179–198.

Hobson, E. S., and J. R. Chess. 1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. Fish. Bull., U.S., 74:567–598.

Jones, L. G. 1971. Studies on selected small herbivorous invertebrates inhabiting *Macrocystis* canopies and holdfasts in southern California kelp beds. Pp. 343–367 *in* The biology of giant kelp beds (*Macrocystis*) in California. (W. J. North, ed.), Beih. Nova Hedwigia 32, xv + 600 pp.

Leighton, D. L. 1971. Grazing activities of benthic invertebrates in southern California kelp beds. Pp. 421–453 *in* The biology of giant kelp beds (*Macrocystis*) in California. (W. J. North, ed.), Beih. Nova Hedwigia 32, xv + 600 pp.

Limbaugh, C. 1955. Fish life in the kelp beds and the effects of harvesting. Univ. Calif. Inst. Mar. Res., IMR Ref. 55-9.

Lowry, L. F., A. J. McElroy, and J. S. Pearse. 1974. The distribution of six species of gastropod mollusks in a California kelp forest. Biol. Bull., 147:386–396.

McDonald, G. W., and J. W. Nybakken. 1978. Additional notes on the food of some California nudibranchs with a summary of known food habits of California species. The Veliger 21:110–119.

McLean, J. H. 1969. Marine shells of southern California. Los Angeles County Mus. Nat. Hist. Science Series, 24:1–104.

Miller, D. J., and J. J. Geibel. 1973. Summary of blue rockfish and lingcod life histories: a reef ecology study; and giant kelp, *Macrocystis pyrifera,* experiments in Monterey Bay, California. Calif. Dep. Fish Game, Fish Bull., 158:1–137.

Mooers, M. G. 1982. Diet and reproductive biology of the rocky intertidal prosobranch gastropod *Tricolia pulloides.* The Veliger 24:103–108.

North, W. J. 1971. Introduction and background. Pp. 1–96 *in* The biology of giant kelp beds (*Macrocystis*) in California. (W. J. North, ed.), Beih. Nova Hedwigia 32, xv + 600 pp.

Pearse, J. S., and L. F. Lowry. 1974. An annotated species list of the benthic algae and invertebrates in the kelp forest community at Point Cabrillo, Pacific Grove, California. Coast. Mar. Lab., Univ. Calif., Santa Cruz, Tech. Reprt., 1:1–73.

Peterson, C. H. 1982. Clam predation by whelks (*Busycon* sp.): experimental tests of the importance of the prey size density, and seagrass cover. Mar. Biol., 66:159–170.

Quast, J. C. 1968. Observations on the food of the kelp-bed fishes. Pp. 109–143 *in* Utilization of kelp-bed resources in southern California. (W. J. North and C. L. Hubbs, eds.), Calif. Dept. Fish and Game, Fish Bull., 139.

Rasmusson, E. M., and J. M. Wallace. 1983. Meteorological aspects of the El Nino/Southern Oscillation. Science, 222:1195–1202.

Riedman, M., A. H. Hines, and J. S. Pearse. 1981. Spatial segregation of four species of turban snails (Gastropoda: *Tegula*) in Central California. The Veliger, 24:97–102.

Rosenthal, R. J., W. D. Clarke, and P. K. Dayton. 1974. Ecology and natural history of a stand of giant kelp, *Macrocystis pyrifera* off Del Mar, California. Fish. Bull., U.S., 72:670–684.

Schmitt, R. J. 1982. Consequences of dissimilar defenses against predation in a subtidal marine community. Ecology, 63:1588–1601.

———, S. W. Osenberg, and M. G. Bercovitch. 1983. Mechanisms and consequences of shell fouling in the kelp snail, *Norrisia norrisi* (Sowerby) (Trochidae): indirect effects of octopus drilling. J. Exp. Mar. Biol. Ecol., 69:267–282.

Smith, R. L. 1983. Peru coastal currents during El Nino: 1976 and 1982. Science, 221:1397–1399.

Stewart, J. G., and B. Myers. 1980. Assemblages of algae and invertebrates in southern California *Phyllospadix*-dominated intertidal habitats. Aquatic Botany, 9:73–94.

Stoner, A. 1982. The influence of benthic macrophytes on the foraging behavior of pinfish, *Lagodon rhomboides* (Linnaeus). J. Exp. Mar. Biol. Ecol., 58:271–284.

Vince, S., I. Valiela, N. Backus, and J. M. Teal. 1976. Predation by the salt marsh killifish *Fundulus heteroclitus* (L.) in relation to prey size and habitat structure: consequences for prey distribution and abundance. J. Exp. Mar. Biol. Ecol., 23:255–266.

Watanabe, J. M. 1984. The influence of recruitment, competition, and benthic predators on spatial distributions of three species of kelp forest gastropods (Trochidae:*Tegula*). Ecology, 65:920–936.

Wing, B. L., and K. A. Clendenning. 1971. Kelp surfaces and associated invertebrates. Pp. 319–339 *in* The biology of giant kelp beds (*Macrocystis*) in California. (W. J. North, ed.), Beih. Nova Hedwigia 32, xv + 600 pp.

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Two New Tiger Beetles of the Genus *Cicindela* from Western United States (Cicindelidae: Coleoptera)

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Abstract.—Two new subspecies of *Cicindela* are described: *C. scutellaris yampae* of northwestern Colorado, and *Cicindela formosa rutilovirescens* of eastcentral New Mexico. Both subspecies are found at the periphery of the ranges of their respective species. This study traces their migration into their present locations in an attempt to define the forces that cause changes leading to subspeciation. *C. scutellaris* is retained as a species group because of the singularity of parts within the internal sac of the aedeagus in the male genitalia. *C. formosa* is significantly different in both male and female genitalia from other members of Rivalier's Group VII so that it constitutes a separate group of its own. Rivalier's Group VII should be renamed the *Purpurea* Group.

The two subspecies described in this paper belong to the tiger beetle species *Cicindela scutellaris* and *C. formosa.* They represent populations located at the limit of the known ranges of these species where contact with other populations has not happened for a long time. Thomas Say described *C. formosa* (1817:19) and *C. scutellaris* (1823:40) from midwestern United States populations that were found sympatrically in sand blowouts, or, as Say called these, "sand alluvions." Both species have extensive ranges sufficiently varied to have resulted in subspeciation. It can be generalized that wherever *C. formosa* is found *C. scutellaris* will occur, but the reverse is not always so because *C. scutellaris* has extended its range into southeastern United States by invading sandy woodlands.

Key to the Subspecies of *Cicindela scutellaris*

1. Bicolored: Head and pronotum bright green, blue-green or blue: elytra from a bright red (sometimes alutaceous), to a darker red 2
– Unicolored, where head, pronotum and elytra are the same background color, sometimes with variations 3
2. Elytra immaculate ..... *scutellaris*
– Elytra with a continuous white maculation at outer edge, with a confused area at middle band position; rarely reduced to broad spots at outer edge ..... *yampae*
3. Color bright to dark red, sometimes suffused with green 4
– Color bright green to deep violet-blue. Variable in size depending on subspecies 6
4. Maculation consisting of white dots on outer edge of elytra ..... *lecontei*
– maculation connected at outer edge of elytra 5
5. Broad maculation at outer edge of elytra, with a non-confused broadened middle area ..... *criddlei*

– Maculation reduced to outer edge dots, infrequently narrowly connected ..... *rugifrons*

6. Smaller (10–11 mm long). Dark blue, blue-green or green, sometimes with apical dots ..... *unicolor*
– Larger (11.5–12.5 mm long) 7
7. Color purplish or blue-green ..... *rugata*
– Color yellow-green ..... *flavoviridis*

Cicindela scutellaris yampae, new subspecies

Figure 1 (1)

Holotype.—Male, in the collection of the American Museum of Natural History (AMNH), New York, NY: collected by Mont A. Cazier, September 1953.

Locality.—Maybell Sand Hills which lie between two and 6 km east of Maybell, Moffat County, Colorado. All specimens of the type series were captured in this region. The first 51 specimens by M. A. Cazier in 1953. The remaining specimens of this series were collected between June 1959 and April 1983.

Type series.—There are 370 specimens in the series, distributed as follows: Holotype and 26 paratypes in the collection of the AMNH, New York, NY; allotype female and 80 paratypes (41 ♂, 39 ♀) in my collection designated the NLRC by Arnett et al. (1969:28). The remainder are in the following collections: two at the National Museum of Natural History (NMNH), Washington, DC; two at the California Academy of Sciences (CAS), San Francisco, CA; Walter Johnson, Minneapolis, MN, 13 specimens; David W. Brzoska, Lawrence, KS, 149 specimens (88 ♂, 61 ♀); Howard P. Boyd, Vincentown, NJ, 37 specimens (21 ♂, 16 ♀).

Description.—Medium size, robust; head and pronotum bluish-green, elytra red with golden birefringence, and broad band of maculation along outer edge which broadens out into confused pattern where middle band would enter normally.

Head: Color mostly bright bluish-green, more green at vertex and near eyes, interocular space nearly blue; only slightly wrinkled at vertex, more so on frons; interocular striae not deep; frons punctured and bearing many decumbent setae; setae between eyes nearly erect but spaced in growth of medium density; clypeus green, blue toward the outer edges, bare; labrum white, outer edges dark, six long white setae near outer edge, tridentate and extended forward but less than half as long as wide; penultimate labial segment longest, heavily setose and metallic blue in color, terminal segment similarly pigmented but bare; segments of labral palpi metallic blue, second segment longest and heavily setose, outer two bare except for a few setae near anterior surface of penultimate segment; first four segments of antennae green, first large and covered with many punctures bearing long white erect setae on anterior surface only, length of fourth segment seven-eights that of third.

Thorax: pronotum narrower than head across eyes, wider than long by more than one-fifth; color green, disc golden, margins bluer, wrinkled; median sulcus blue and shallow, crossed with transverse impressions; anterior sulcus blue, deep, micro-reticulated anteriorly only, not wrinkled; posterior sulci also blue and deep; longitudinal row of white, erect setae two-thirds distance from centerline, another row of setae at epipleural edge, recumbent toward center, but distinct from very long sub-epipleurual setae.

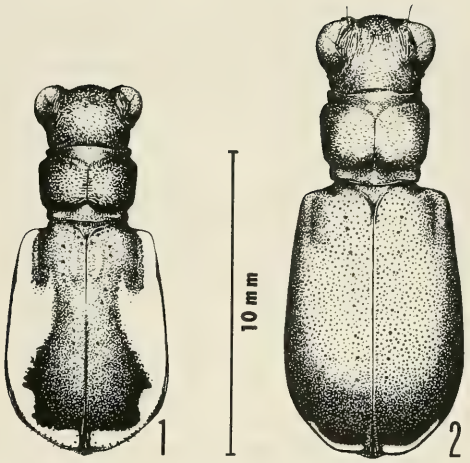

Fig. 1. Dorsal views. 1. *Cicindela scutellaris yampae*, 2. *C. formosa rutilovirescens.*

Elytra: Broad, widest posterior to middle; micro-reticulate and covered with very small impressions, surface transparent in appearance with birefringence of golden green on disc against basic red color; disc with row of very small setigerous punctures near suture; another short row of punctures located in humeral impressions that delimit disc; maculation continuous at outer edge of elytra but lunules and middle band traceable, pattern as in Figure 1 (1); pigment at discal edge of maculation deeper red, almost purple in small impressions.

Venter: Bright greenish-blue throughout; genae with longitudinal stria, glabrous; epimera and coxae with numerous long setae; femora and tibia greenish blue, with long white setae, tibiae more densely covered with setae, tarsal claws nearly as long as last tarsal segment; penial notch present as a slight declivity on penultimate sternite.

Comment.—Females are similar to males, both in size and proportion, but differ in that the frons is nearly glabrous.

Dimensions.—Holotype, male—length 11.8 mm, width 4.9 mm. Allotype, female—length 12.0 mm, width 5.1 mm.

Etymology.—Named for the Yampa River Valley of Utah.

Population variables.—In a population sample of 56 specimens studied in more detail, the most striking variations are in color and maculation.

Color: The head and pronotum are green in 51 specimens, blue in four, and golden green in one. Elytra are red, varying between dark red and golden red, superimposed with varying amounts of green suffusion—the darker the red, the less the green suffusion.

Maculation: In 46 specimens the maculation is connected along the entire margin of the elytra. In four specimens the humeral lunule, or dot, is disconnected from the marginal band. In seven specimens the maculation is reduced to marginal dots, and in two cases, the humeral dots are lacking. In all samples the middle band consists of an expansion from the outer edge toward the center of the elytra, with a confused area at the basal edge in the majority of specimens. In 27 specimens this confused area expands considerably anteriorly toward the base of the elytra

such that these specimens are more heavily maculated than the rest. Of the more heavily maculated specimens 23 have epicentral spots which, in some cases, consist of a narrow vertical line bordered by a purplish-red pigmentation; in two cases the white disappears, but the area is marked by the deeper red color.

Conclusions Based on Faunal Distribution

1. During the glacial periods of the Pleistocene, a broad region of southcentral Wyoming became a refugium for a number of Canadian species of *Cicindela.* The species most sensitive to change developed noticeable characteristics in response to climate change, and possibly through some hybridization. This seems to have been the situation with *C. scutellaris.*

2. A region of northern Montana, centered around Great Falls, was an isolated haven for species from Alberta as they migrated southward ahead of glacial advances. Here, the environmental impact on *C. scutellaris* was slight, thereby inducing only slight color change. Thus, the climate in this region was hardly more severe than today's climate in central Alberta.

3. Isolated populations of *C. scutellaris, C. formosa* and *C. limbata* may still exist in the Bighorn and Powder River Basins. The discovery of such populations would aid in tracing the migratory routes of these species.

Key to the Subspecies of *Cicindela formosa*

1. Elytra broadly maculated 2
– Elytra immaculate or narrowly maculated 4
2. Broad white maculation of elytra consisting of humeral and apical lunules, and a middle band; all narrowly connected at edge 3
– Maculation coalesced into total coverage of elytra ..... *gibsoni*
3. Bright red in color. Midwestern form ..... *formosa*
– Dark brown in color. Eastern form ..... *generosa*
4. Elytra with apical lunule white, often with other lunules pigmented, or lacking. Color dark red with upper half of elytra a deep purple ..... *pigmentosignata*
– Elytra with either narrow apical lunule only or none at all. Color bright red with green birefringence ..... *rutilovirescens*

Cicindela formosa rutilovirescens, new subspecies

Figure 1 (2)

Holotype.—Male, no. 12984 in the collection of the CAS, San Francisco, CA, captured by Mont A. Cazier, October 1953.

Locality.—The type location is in the Mescalero Sands, 55 to 65 km due east of Roswell, New Mexico, in the eastern part of Chaves County, at a mean elevation of 1300 m. The sands trend from southwest to northeast for nearly 50 km, their width varying from 6 to 14 km. The area is made up of low hills, 2 to 3 m high, covered with a short scrub oak (*Quercus harvardi*) which partially stabilizes the sand, although in a few places bare dunes rise to heights not exceeding 8 m. The ground sand is light in color, somehat darker where vegetation growth contaminates it with debris. The innumerable blowouts in the troughs of the oak-covered area are bare.

Type series.—There are 185 specimens from the type area, distributed as follows: Holotype male and three paratypes at the CAS; allotype female and 28 paratypes in the NLRC, collected in October 1953 by M. A. Cazier, in September 1957 by E. Tinkham, and at various times by me from 1960 to 1980. Paratypes are in the private collections of the following individuals: W. D. Sumlin, 12 (3 ♂, 9 ♀); E. V. Gage, 3 (2 ♂, 1 ♀); G. Gaumer, 30 captured in May 1971; D. Brzoska who collected in May and September from 1978 to 1982, 56 (35 ♂, 21 ♀); J. Stamatov, 27, and H. Boyd, 23 specimens which they collected in September 1976.

There are 24 paratypes from locations other than the type area which are distributed as follows: One female from Terry County, TX collected by D. Kelly deposited in the collection of Walter Johnson; eight specimens collected east of Plains, Yoakum County, TX, two of which are in the NLRC; one from SSE of Loco Hills, Eddy County, NM by G. Gaumer in September 1971; three from Portales, Roosevelt County. NM in the East New Mexico University collection; one male in the NLRC collected by J. Sheppard in May 1974 south of Milnesand, Roosevelt County, NM.

Description.—Large in size, form robust, upper surface red, birefringent with green, with only slight indication of maculation at apex of elytra.

Head: Bright golden red vertex finely wrinkled, interocular striae brightly colored red with golden tinges; frons wrinkled and punctate, greenish at edges, bright deep blue toward antennae, punctures with long white setae, nearly recumbent anteriorly, anteriormost setae lying toward vertex, middle setae lying toward sides, and sparse setae between eyes lying generally toward middle; clypeus bright blue, violaceous toward sides; first four segments of antennae green, first segment with three or four setae from middle to apex on outer edge, four or five setae around apex and near base of second segment, with third segment nearly one-third longer than fourth; labrum tridentate, extended forward, one half as long as wide, whitish with outer edge dark, six setigerous punctures near outer edge; long heavily setose penultimate labial segment nearly 1.5 times as long as glabrous last segment, both metallic blue; second labral palpal segment unpigmented with white setae on basal half, 2.1 times longer than penultimate segment and 1.3 times longer than last segment, both of the latter metallic green.

Thorax: Pronotum nearly as broad as head, ratio of width to length = 1.15 and broadest just basal to anterior transverse impression, tapered to rounded posterior angle; surface finely rugose; median sulcus of disc shallow, anterior and posterior sulci deep; color red with golden tinge, more so laterally and at bottom of impressions; two rows of recumbent setae, one near lateral edge, other just above epipleurae; venter bright violaceous blue; all three thoracic sterna and coxae with medium growth of long white setae.

Elytra: Wider at shoulder than head, tapered slightly wider for two-thirds, then broadly rounded to apex; entire elytral surface micro-reticulate, impressed throughout with minute shallow pits, each with slightly raised anterior edge; one row of very small setigerous punctures near suture, not readily seen except under magnification, entire surface with birefringent transparency such that surface appears red when viewed from above, but when viewed from oblique angles it appears greenish; outer edge narrowly bluish green at epipleural ridge; no mac-

ulation except for barely visible narrow band of white representing vestigial apical lunule.

Venter: Deep metallic violaceous blue; genae wrinkled, with a few recumbent setae ventrally and remote from the eyes; all sterna and coxae covered with medium growth of long white decumbent setae; trochanters galbrous except for one long setigerous puncture at apex; femora and tibiae blue, with long white setae; tarsi dull bluish green, each segment with a few pits near apex from which rise long setae; tarsal claws long, those of hind tarsus nearly as long as last tarsal segment; all segments of abdomen sparsely covered with white setae; penial notch symmetrical but shallow.

Dimensions.—Female slightly longer and proportionately broader than the male. Holotype male—Length 12.0 mm, width 5.8 mm. Allotype female—length 16.2 mm, width 6.8 mm.

Etymology.—Named for its primary color red (*rutilis*), and its secondary green (*viridis*) birefringence.

Population variables.—Of 85 specimens studied in detail 13 were completely immaculate. Nearly all the rest appeared to be immaculate also, but actually bore either a minute apical spot, or a very thin white line that paralleled the apical portion of the elytra for a short distance, but not recurved. Only one specimen had markings consisting of a narrow uninterrupted humeral lunule, a thin middle band without recurved tip, the latter connected along the edge to a thin apical lunule.

The degree of color transparency is varied. Nearly one third of the specimens studied had a deeper color. When viewed from above they appeared less birefringent than the lighter colored specimens.

Hybrid populations.—The slight variations in color and maculation reported above suggest that intergradation of this form with *C. f. formosa* has occurred where the Llano Estacado blends into the Great Plains to form the hybrid population of *rutilovirescens* × *formosa.* Such hybrids were taken by G. Gaumer in Texas, both at Muleshoe, Bailey County and north of Sudan, Lamb County in October 1971. D. Brzoska located another hybrid group north of San Jon, Quay County, New Mexico. Of six specimens from San Jon, two are similar to ssp. *rutilovirescens,* one with a high degree of birefringence, the other a darker red; another is similar to ssp. *formosa,* whereas the other three have narrower maculation with short middle band, one with some birefringence.

On the Status of *Cicindela formosa manitoba*

In the northwest region of the Great Plains, in a broad area encompassing parts of the United States and Canada, the maculation of *Cicindela formosa* broadens until the limit is reached where the elytra are nearly white. *C. f. manitoba* was described by C. W. Leng (1902:137) from broadly marked Manitoba populations, many years before still more broadly marked populations were discovered farther west, in Saskatchewan, and subsequently described by W. J. Brown (1940:181) as *Cicindela formosa gibsoni.* This last subspecies represents the broadest maculation form, a condition mentioned earlier as having been associated with migration to an area where such a type of maculation was common to several related species of *Cicindela. C. f. gibsoni* developed through isolation, whereas *manitoba* is a hybrid created wherever ssp. *gibsoni* and ssp. *formosa* met upon returning

north during Pleistocene interglacials. Therefore, the name *manitoba* has no status in the nomenclature, and as such becomes a junior synonym of *C. formosa.*

Systematics of *Cicindela scutellaris* and *Cicindela formosa*

An early attempt to classify the Cicindelidae of the United States was made by J. L. LeConte (1856:33–40). He placed *Cicindela scutellaris* in a Group VI with *C. pulchra, C. lecontei,* and *C. nigrocoerulea. Cicindela formosa* was placed in Group VII with *C. ancocisconensis, C. venusta* (=*C. lengi), C. vulgaris* (=*C. tranquebarica*) and *C. fulgida.* The LeConte classification was based largely on similarities of markings, and to a lesser extent on punctation and pilosity. Leng (1902: 124–125), in his revised classification, altered the LeConte scheme by placing *C. scutellaris* in a group by itself. Leng (1902:135) placed *C. formosa* with *C. lateasignata* and *C. tenuicincta.* W. Horn (1926:262) took a broader view by combining some Nearctic Cicindelidae into a *Formosa—purpurea—oregona* Group. Here, he included both *C. scutellaris* and *C. formosa.* In his Catalogue, Leng (1920:40) reflects the Horn viewpoint.

In 1954, Rivalier revised the Nearctic genus *Cicindela* under an earlier stated intention (Rivalier 1950:15) to dismember the classical genus *Cicindela* into a number of new genera. The primary method to accomplish this was based on a comparative study of the structures within the aedeagus. The intention of my paper is to go a step further and use the genitalia of both sexes. The aedeagi of the males, and the female external genitalia (those parts used to dig holes in which to deposit eggs), are shown in Figures 2 through 5. The definition of terms to describe the aedeagus are the same used earlier (Rumpp 1967:134). Those used to describe the female parts are the same as used by V. M. Tanner (1927).

Genitalia of *Cicindela scutellaris*

Figures 2 and 3

Male.—Nineteen aedeagi were examined, some in the resting position, some everted. Six were mounted on slides, the rest preserved in alcohol. These aedeagi were from specimens taken in Colorado, Nebraska, Oklahoma, and Texas.

The penis is arched, and the central bulge is long to accomodate an unusually long internal sac. The apex is nearly concentric when viewed from the inner side. The apical ridges are long but not prominent. The bulges on the mid-dorsal and mid-ventral sides are equal in size, but the ventral one is lower.

The internal sac is long, as noted by Rivalier (1954:252). The structures that form a central plate are feebly developed, so much so that the tip, or tooth that caps the central plate, is reduced to a very small scutum (Fig. 2, c and d). Other structures are well developed, especially so in the great length of the large stiffening rib, and long filiform flagellum with its loose basal whorl. The elongated sac resembles the general design found in species of the subgenus *Habroscelimorpha,* also mentioned by Rivalier (1954:252), and depicted, in part, by Rumpp (1957: 146–147), but it differs internally where the flagellum of *C. scutellaris* does not sustain a membrane.

In the copulatory evaginated position, the internal sac of *C. scutellaris* everts at an acute angle of about 25° from the centerline of the penis. This is similar to the process in most of the species of *Cicindela* (sensu Rivalier). The everted

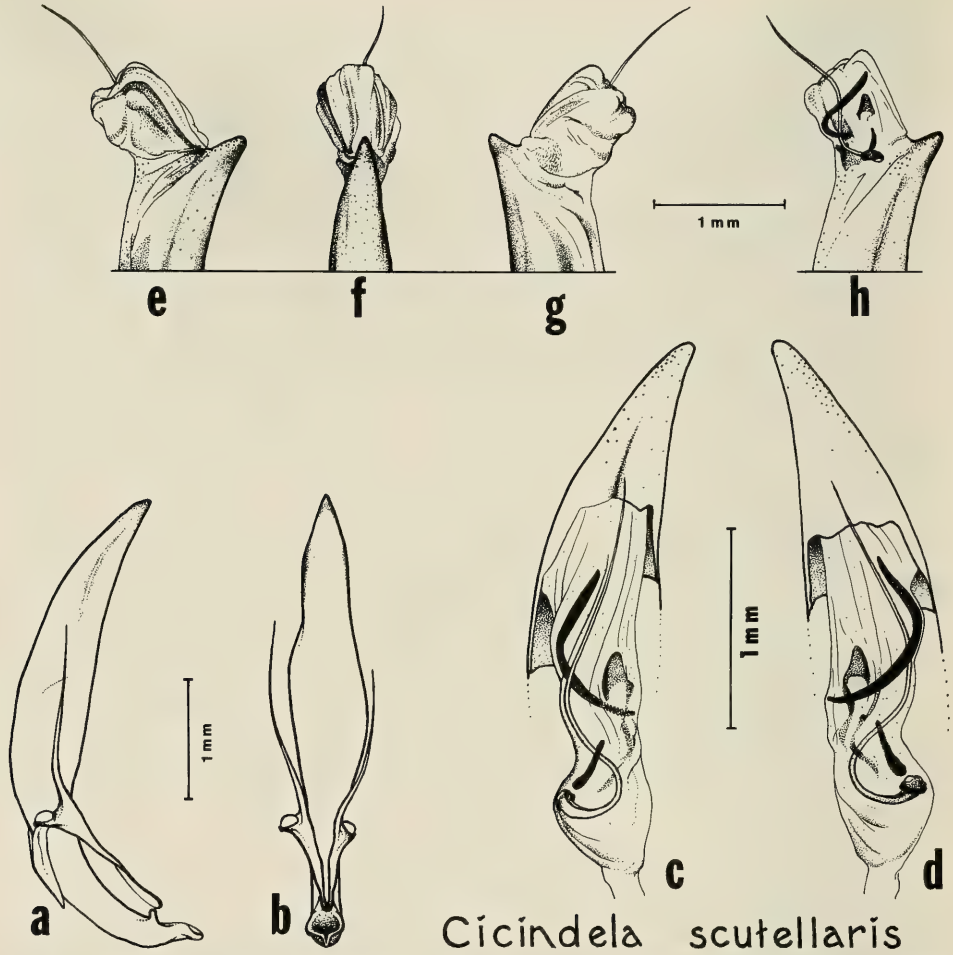

Fig. 2. Aedeagus of *Cicindela scutellaris*. View *a* and *b* of the dorsal and inner sides of the penis, ssp. *scutellaris* (Lakeside, NE); views *c* and *d* of the dorsal and ventral sides of the internal sac, ssp. *rugata* (Nacogdoches, TX); *e, f,* and *g* are views of the everted sac, ssp. nov. (Maybell, CO—type location); *h* is a through view of the everted sac showing location of the sclerites, ssp. *scutellaris* (Boise City, OK).

convolutions are uncomplicated, and the external fields are not pronounced. There is no apical fold near the ventral side. This departure from other species may have induced advanced development of the flagellum and large stiffening rib, while concurrently inducing atrophy of the tooth structure.

Female.—The external genitalia are shown in Fig. 3. The cleft in the hypopygium is V-shaped, much as it is in closely related species of the *Purpurea* Group. The styli are long, and the tip of the proctiger is wider at the top than in either *C. formosa* or the species of the *Purpurea* Group.

Conclusion.—The placement of *C. scutellaris* in Rivalier's phylogeny is correct. However, the slight morphological departure from *Cicindela* (sensu Rivalier) does not warrant his erecting the separate subgenus *Pachydela* for this one species. The

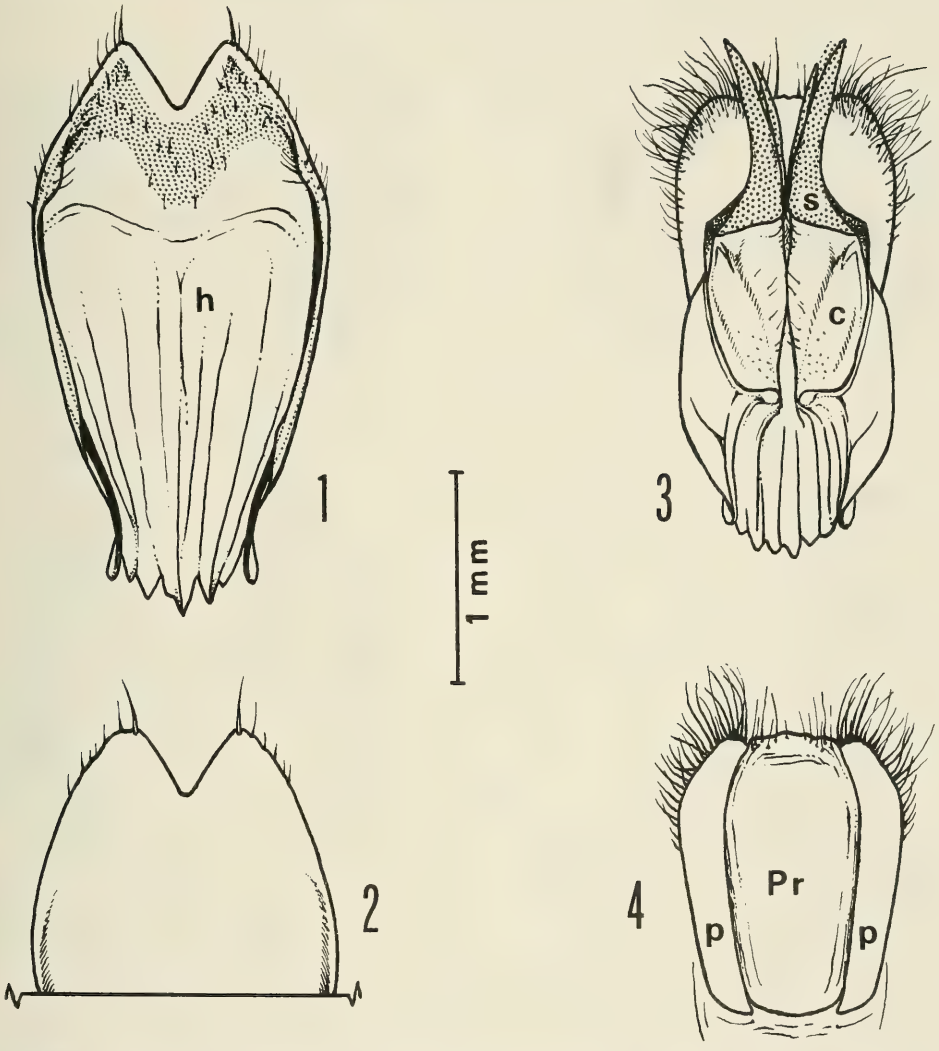

Fig. 3. *Cicindela scutellaris yampae,* external female genitalia. 1. Dorsal, or inside view of sternum eight (*hypopygium*); 2. Ventral, or outer view of sternum eight—upper part only; 3. Ventral view of second gonocoxa (*coxite*) and second gonopophysis (*stylus*); 4. Dorsal view of syntergum 9 and 10 (*proctiger* and *paraprocts*).

name *Pachydela* remains a junior synonym of *Cicindela* as recorded in the Checklist of Cicindelidae by H.P. Boyd et al. (1982:6).

Genitalia of *Cicindela formosa*

Figures 4 and 5

Male.—Twenty-seven aedeagi were examined in both the resting and everted positions. Of these, 12 were mounted on slides, and 15 were preserved in alcohol. These organs were extracted from specimens collected in Colorado, Oklahoma, Texas, and New Mexico.

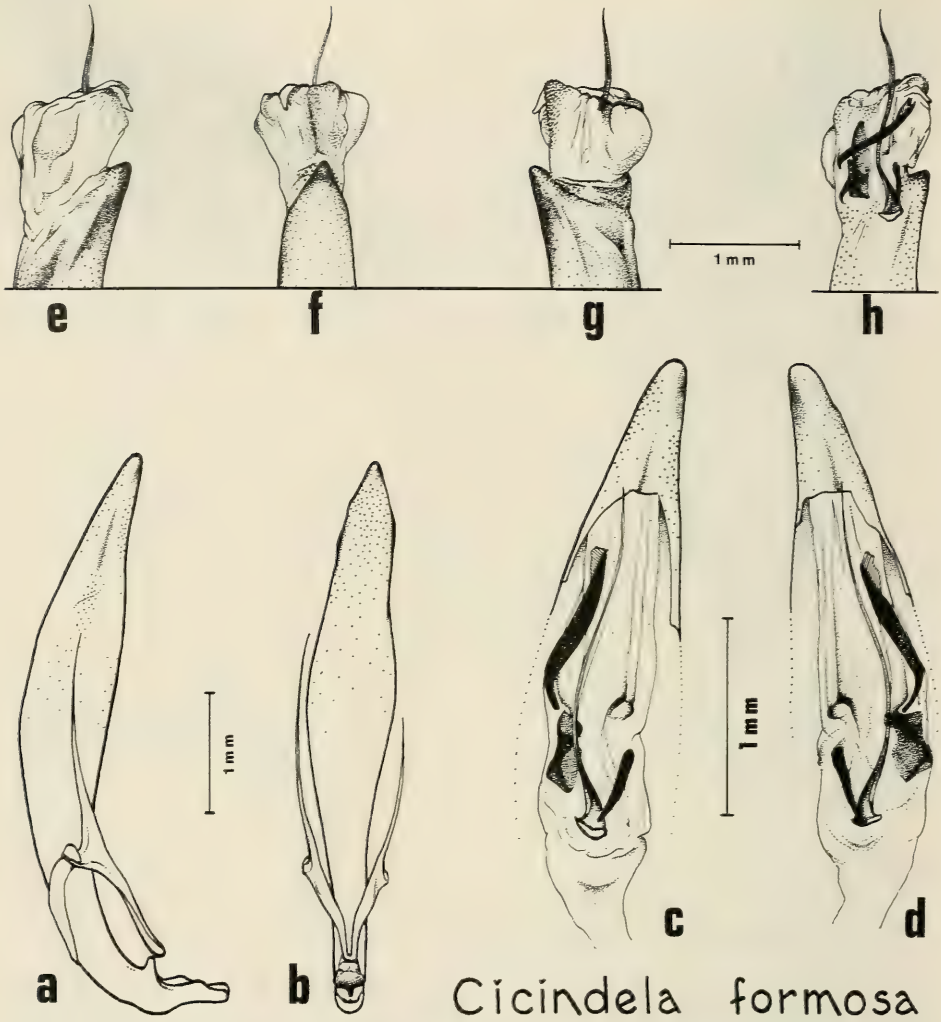

Fig. 4. Aedeagus of *Cicindela formosa.* View *a* of the dorsal side of the penis; *b* of the inner side; *c* and *d* the dorsal and ventral sides of the internal sac, ssp. nov. (Mescalero Sands, NM—type location); *e, f, g,* and *h* are views of the everted sac, ssp. *gibsoni* (Maybell, CO).

The penis of *C. formosa* is proportionately small for a tiger beetle of its size (Fig. 4, a and b). It is smooth on the exterior, and only slightly arched. The lateral ridges are not pronounced. The overall shape is nearly concentric, with no bulges on either the dorsal or ventral side.

Rivalier (1954:253) erected Group VII, designating *C. formosa* as the type species. Included in this group were *C. purpurea, C. limbalis,* and *C. sexguttata,* all because the penis was not arched, the internal sac was provided with a thin flagellum, and a median tooth was claimed to be absent. Such a description seems to fit *C. formosa* to some degree, as shown in Fig. 4. However, it does differ radically from the other species placed in Group VII because is does not possess a median tooth, whereas the others do.

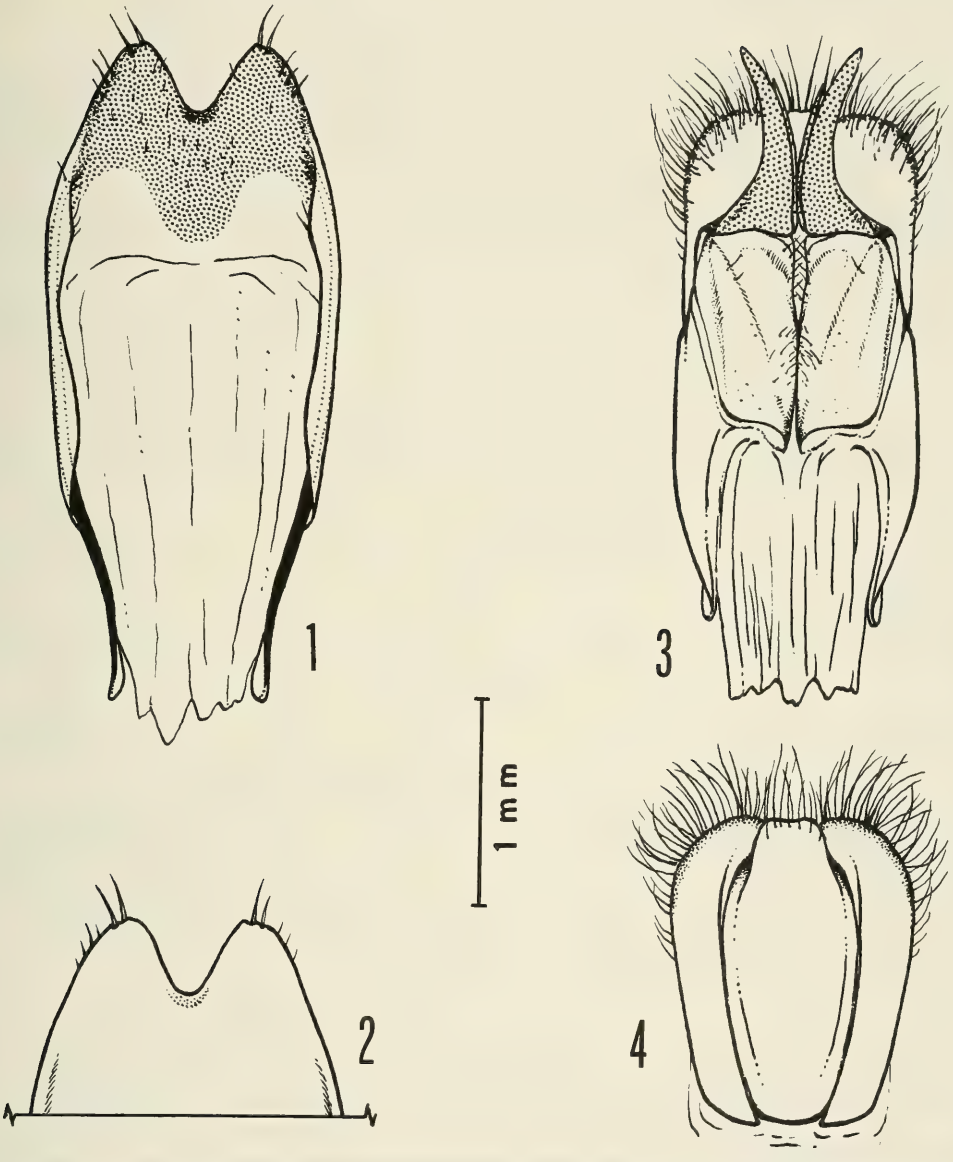

Fig. 5. *Cicindela formosa rutilovirescens,* external female genitalia. 1. Dorsal, or inside view of sternum eight (*hypopygium*) h; 2. Ventral or outer view of sternum eight—upper party only; 3. Ventral view of second gonocoxa (*coxite*) c and second gonopophysis (*stylus*) s; 4. Dorsal view of syntergum 9 and 10 (*proctiger and paraprocts*) Pr&p.

Another significant departure from other species in Rivalier's Group VII is the unique development of the everted sac shown in Fig. 4 (*e, f, g,* and *h*). In *C. formosa* the internal sac everts apically, nearly in line with the centerline of the penis, and not at the angle so typical of the other species in Rivalier's Group VII. The eversion of the *C. formosa* sac is at an angle similar to the eversion of the sac in species of the subgenus *Habroscelimorpha,* but otherwise differs from these

Fig. 6. Map of a portion of southwestern United States showing location of some new tiger beetles of the Genus *Cicindela*.

by having a median tooth and a stubby-based flagellum that does not sustain a large membrane.

Female.—The external female genitalia are shown in Fig. 5. The outstanding feature is the curved bottom of the hypopygium notch. This is a radical departure

from all other species in Rivalier's Group VII; these other species have an acute angle to their hypopygium notches.

Conclusion.—From an evolutionary standpoint, *C. formosa* fits into a singular niche of the subgenus *Cicindela.* It is a species with adults equal in size to, or larger than, those of the *Longilabris, Pulchra,* or *Tranquebarica* Groups. Ecologically it is adapted to the various climates and environments of the upper North American continent where it remains fixed in a sand-dwelling niche. It has an extensive distribution across the United States and Canada, from the Rocky Mountains to the eastern seaboard. The generic features of this species have few attributes to fix its ancestral type with other extant species. Therefore, it must be assumed that its derivation stems from great antiquity. It is a singular development of the Nearctic regions.

Phylogenetically *Cicindela formosa* fits between the *Scutellaris* Group (sand blowout habitat; long internal sac of the aedeagus, with long unsustained flagellum and atrophied tooth), and the *Purpurea* Group (coarse sand habitat; internal sac of the aedeagus with a very small tooth and a short sinuous flagellum).

Referenced Locations

Figure 6

Locations are shown on this map with reference to *C. scutellaris yampae* and *C. formosa rutilovirescens.*

Literature Cited

Arnett, R. H. and Samuelson, G. A. 1969. Directory of Coleoptera Collections of North America (Canada through Panama), 123 pp.

Boyd, H. P. and Associates 1982. Checklist of the Cicindelidae. Plexus Publishing, Inc., 31 pp.

Brown, W. J. 1940. Some new and Poorly Known Species of Coleoptera. Canadian Entomologist, 72:183–184.

Horn, W. 1926. S. Schenkling on Carabidae—Cicindelidae, 85, W. Junk Coleopterum Catalogus, ed. pp. 258–302.

LeConte, J. L. 1856. Revision of the Cicindelidae of the United States. Trans. Am. Phil. Soc., II (New Series):27–62.

Leng, C. W. 1902. Revision of the Cicindelidae of Boreal America. Trans. Am. Entom. Soc., 28: 93–190.

——— 1920. Catalogue of the Coleoptera of America North of Mexico, compiled by John D. Sherman Jr., Mount Vernon, NY. 470 pp.

Rivalier, E. 1950. Démembrement du Genre *Cicindela* Linné—Faune Paléarctique. Revue Franç. d'Entom., 17:217–244.

——— 1954. Démembrement du Genre *Cicindela* Linné—Faune Nearctique. Revue Franç. d'Entom., 21:248–268.

Rumpp, N. L. 1957. Notes on the *Cicindela praetextata—californica* Complex; Description of New Subspecies from Death Valley, California. Bull. So. Calif. Acad. Sci., 58:144–154.

——— 1961. Three New Tiger Beetles of the Genus *Cicindela* from Southwestern United States. Bull. So. Acad. Sci., 60:165–187.

———1967. A New Species of *Cicindela* from Idaho. Proc. Calif. Acad. Sci., 35:129–140.

Say, T. 1817. American Entomology. Journ. Acad. Nat. Sci. of Phila., 1:19–23.

——— 1823. Descr. of New Species of Coleoptera from an Expedition to the Rocky Mnts. Journ. Acad. Nat. Sci. of Phila., 3:139–216.

Tanner, V. M. 1927. A Prelim. Study of the Genitalia of Female Coleop. Trans. Amer. Entom. Soc., 53:5–50.

Wallis, J. B. 1961. The Cicindelidae of Canada. Univ. of Toronto Press, 74 pp.

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Coyote Diets, Five Years Later, at Cuyamaca Rancho State Park

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Abstract.—Food habits of coyote (*Canis latrans*) on East Mesa, Cuyamaca Rancho State Park, San Diego County, California were studied by analysis of scats. Remains of pocket gopher (*Thomomys bottae*), mule deer (*Odocoileus hemionus*), vole (*Microtus californicus*), ground squirrel (*Spermophilus beecheyi*), and white-footed mouse (*Peromyscus* spp.) were predominate in scats collected from November 1983 to July 1984. Five years earlier coyote on East Mesa were reported to feed primarily on beaver (*Castor canadensis*), white-footed mouse, opossum (*Didelphis virginiana*), pocket gopher, mule deer, and badger (*Taxidea taxus*). Explanations are offered for the differences noted.

The coyote (*Canis latrans*) has been described as an opportunistic predator (Bekoff 1977). In California, Ferrel et al. (1953) found rodent in 49%, rabbit in 29%, deer in 18%, and carnivore in 4% of 2222 coyote stomachs. MacCracken (1981) noted that when leporids were poorly represented in western coyote diets, the proportion of vole, pocket gopher, or ground squirrel was usually high. Bowyer et al. (1983) reported on coyote diets over a twenty month period (June 1977–January 1979) from the East Mesa area of Cuyamaca Rancho State Park, California. Leporids were found in only 1% of their sample while beaver (*Castor canadensis*) was present in 44% of 223 scats. Carnivores were present in 33%, opossum (*Didelphis virginiana*) in 24%, pocket gopher (*Thomomys bottae*) in 22%, and mule deer (*Odocoileus hemionus*) in 21% of the coyote droppings analyzed by Bowyer et al. (1983).

A review of 57 coyote diet studies (list available from the author) indicates that the earlier East Mesa coyote study (Bowyer et al. 1983; Bowyer, pers. comm.) recorded the highest frequency of opossum, beaver, gray fox (*Urocyon cinereoarenteus*), bobcat (*Lynx rufus*), long-tailed weasel (*Mustela frenata*), and badger (*Taxidea taxus*) in any North American study, as well as the only records of mountain lion (*Felis concolor*) and man (*Homo sapiens*). The present study investigated whether this unusual coyote diet persists at Cuyamaca Rancho State Park.

Methods

East Mesa encompasses about 800 hectares of upland meadows and oak-pine woodlands at an elevation of 1525 m; the site is in the southern part of Cuyamaca Rancho State Park, San Diego County, California and is surrounded by lower elevation chaparral (Bowyer and Bleich 1980). The Laguna Mountain area of Cleveland National Forest is to the east and the towns of Guatay and Descanso are located about 4.5 km south and 5.5 km southwest, respectively. Weather data

are available for over 60 years from Descanso Ranger Station (elevation 1066 m). A rainfall gauge is also at park headquarters, 1.5 km west of East Mesa at an elevation of about 1280 m.

Scats were collected along the East Mesa Fire Road on East Mesa on 19 November 1983 (N = 26), 27 January 1984 (N = 25), 9 April 1984 (N = 28), and 7 July 1984 (N = 35). All scats collected were greater than 20 mm in diameter which should exclude gray fox droppings, but also excludes about half of the coyote scats produced in the area (Danner and Dodd 1982). Scats that might be from bobcat (regular annular constrictions) were not collected.

Scats were dried at 80°C for 48 hrs to destroy tapeworm stages and then washed in a flour sifter (mesh opening about 1.7 mm) under running water. Most of the bones, teeth, and claws were separated from the hair by placing the washed material in water in an enamel tray and floating off the hairs into the sifter. Hair and heavier material were separately dried and analyzed. The apparatus was carefully cleaned between scat preparations. Claw, bone, and tooth material were identified to species using reference collections at California State University Fullerton (CSUF). A key to rodent incisors also aided the process (Weintraub and Shockley 1980). Mayer (1952), Moore et al. (1974), and Stains (1958) were used for hair identification as well as a hair slide collection from CSUF's specimens. Intact tufts of hair from unidentified prey were stored on two-sided sticky tape placed on blue paper for color viewing and measurements of the hairs. If further microscope viewing was needed, they were cleaned in carbon tetrachloride and scale pattern molds of the hair made using techniques of Hilton and Kutscha (1978). Hairs were then immersed in xylene for ½ hr before permanent mounting on slides. Hair slides were viewed under polarized-light microscopy to accentuate the medullary features. Voucher materials were kept for future reference.

Differences between seasons or between studies in the proportion of scats with a particular prey item were analyzed by an exact test for 2 × 2 contingency tables (Wells and King 1980). Significance was set at the 5% probability level. An expanded species list was available from Bowyer for the 1977–1979 East Mesa study and accounts for most of the "Bowyer, pers. comm." citations in this paper.

Results

Table 1 compares coyote prey items found in the present study with those found in the 1977–1979 study. I recorded 17 mammal prey species including a tentative identification of house cat (*Felis catus*) and Bowyer et al. (1983) recorded 26 mammal prey species (includes both *Neotoma fuscipes* and *N. lepida*). I had 6 unidentified rodent items. Seasonal differences occurred in the proportion of scats containing a given prey in 1983–1984. Between the November and January samples the proportion of seed showed a significant reduction and the proportion of vole (*Microtus californicus*) significantly increased in the droppings. Between the April and July samples, both vole and white-footed mouse (*Peromyscus* spp.) showed significant reductions in scat occurrences while the proportion of ground squirrel (*Spermophilus beecheyi*) and seed material significantly increased. Neither pocket gopher nor deer showed significant changes in their proportions in coyote droppings between sampling periods, but deer showed a higher proportion for the fall and summer samples.

Three of the six most commonly recorded mammal prey species in the 1977–

Table 1. Coyote food items (% occurrence in scats; tr = <0.5%) based on analysis of 223 droppings from June 1977 to January 1979 (=BOW: Bowyer et al. 1983; Bowyer, pers. comm.) and on analysis of 114 scats from November 1983 to July 1984 (=WEI: current study) from the East Mesa area of Cuyamaca Rancho State Park, San Diego Co., California.

Prey item	Study		Prey item	Study	
	BOW	WEI		BOW	WEI
Mammals					
Didelphis virginiana	24	—	*Procyon lotor*	2	1
Scapanus latimanus	—	3	*Mustela frenata*	2	—
Eumops perotis	tr	—	*Taxidea taxus*	11	—
Lepus californicus	tr	—	*Spilogale gracilis*	1	—
Sylvilagus auduboni	1	—	*Mephitis mephitis*	2	1
Eutamias merriami	1	1	*Felis concolor*	3	—
Spermophilus beecheyi	3	24	*Lynx rufus*	3	1
Sciurus griseus	2	1	*Felis catus*	—	1 (?)
Thomomys bottae	22	64	*Odocoileus hemionus*	21	41
Perognathus californicus	1	—	*Homo sapiens*	tr	—
Dipodomys agilis	tr	1			
Castor canadensis	44	—			
Reithrodontomys megalotis	—	4	Birds	3	6
Peromyscus spp.	26	19			
Neotoma spp.	1	4	Reptiles	4	12
Microtus californicus	—	32			
Canis latrans	5	1	Arthropods	34	47
Urocyon cinereoargenteus	3	—			
Bassariscus astutus	1	1	Vegetation	84	33

1979 study were not recorded from coyote droppings in 1983–1984 (i.e. beaver, opossum, and badger); five of these six (*Peromyscus* spp. the exception) showed significantly different frequencies of occurrence between the two studies. Of the five most common mammal prey species encountered in coyote droppings in 1983–1984, one species was not recorded in 1977–1979 (i.e. vole); four of these five species (*Peromyscus* spp. the exception) showed significantly different proportions in coyote scats between the two studies.

Discussion

Coyote on East Mesa fed largely on gopher, deer, vole, and ground squirrel in 1983–1984, a pattern similar to other diets from western areas with low leporid intake (e.g., Hawthorne 1972; Murie 1940; Weaver 1980). This study documents the highest intake of pocket gopher of any of 57 previous coyote diets. High populations of deer (approximately 200) and ground squirrel were noted on the East Mesa area in the late 1970s (Bowyer and Bleich 1980), and were still prevalent in and around this area during the present study. Overgrazing by cattle in the 1950s and a major chaparral fire during the period may have favored these species as well as pocket gopher.

Seasonal dietary shifts by southern California coyote were reported by Ferrel et al. (1953). Vegetation was a major fall food item while animal consumption was highest in spring and deer intake highest in the summer. Both East Mesa studies found large amounts of vegetation taken most frequently during the fall.

Deer intake by coyote appeared to increase during the summer months, presumably corresponding to fawn production.

The two East Mesa coyote studies differ significantly in the proportion of many of the prey items in the scats. Coyote from East Mesa appear to have fed on rare or restricted prey during 1977–1979 (e.g., beaver, badger, and mountain lion). San Diego County is outside the historic range of the beaver (Tappe 1942). However, four beaver were released near Cuyamaca Rancho State Park in 1945 (Calif. Fish and Game, no date) as part of a statewide transplant program. The nearest beaver sites in the late 1970s were located on the Sweetwater River, about 3 km west of East Mesa. Only one colony was known to be in the park (at the Green Valley campground) with two colonies located south of the park boundary in 1978 (Treanor, pers. comm.). Beaver were last seen in the park in 1979 (Treanor, pers. comm.; Bowyer, pers. comm.) and last seen below the park in 1981 (Treanor, pers. comm.).

The California Department of Fish and Game carried out a large-mammal trapping program in the late 1970s to the east of East Mesa. Gould (pers. comm.) estimated, based on trapping data from that program, that badger were present here in densities of 1.3 animals per sq km. Badger are rarely recorded as coyote prey. Rathbun et al. (1980) observed coyote killing a young badger by cooperative predation under low prey availability conditions. Gould (pers. comm.) also estimated that mountain lion density was 0.1 to 0.3 per sq km in the trapping area. They were recorded in coyote scats from three separate seasons by the 1977–1979 study (Bowyer, pers. comm.). A mountain lion can kill a coyote (Gianini, 1935).

Opossum were common on East Mesa in the late 1970s (Curto, pers. comm.; Bowyer, pers. comm.). Their present abundance is unknown. Although opossum were reported taken by coyote in about one sixth of the other reviewed diet studies, their frequency in coyote scats or stomachs never exceeded 3%. Whiteman (1940) found that captive coyote rejected opossum, insectivora, and weasel flesh. This discussion suggests that coyote may have been under food stress during 1977–1979 and were utilizing uncommon, perhaps less appetizing, and potentially dangerous prey species in spite of the apparently high deer, ground squirrel, and probably pocket gopher populations in the park.

The 1977–1979 study occurred at the end of a period of below average rainfall and during the very heavy 1978 rainfall year. Rainfall (% of normal) at Descanso Ranger Station was as follows: 1973 = 96%; 1974 = 86%; 1975 = 91%; 1976 = 103%; 1977 = 86%; 1978 = 199%; 1979 = 126%; 1980 = 193%; 1981 = 75%; 1982 = 168%; 1983 = 185% (U.S. Dept. Commerce 1973–1983). The present study occurred during an unusually low spring rainfall period, as only 7 cm of rain was recorded at park headquarters from January to June 1984. Vole were not recorded as food items in the earlier East Mesa study but they were a major prey item in the current study. Recent rainfall patterns may have favored high vole populations in the park. Vole are also known to exhibit cyclic population fluctuations (Pearson 1966). Vole were considered to be the most important rodent prey for California coyote (Ferrel et al. 1953) and changes in the population of this species might influence food selection by coyote. Blankenship (1982) found no vole in 5430 trap nights between December 1979 and December 1980 on a burned pine forest site on East Mesa. Vole made up a small part (1%) of the diet of spotted owl (*Strix occidentalis*) in the park in 1978 and 1979 while most of

the owl diet was dusky-footed woodrat (*Neotoma fuscipes,* 33%), white-footed mouse (31%), and gopher (8%) (Barrows 1980).

Another environmental factor that may have influenced prey populations is controlled burns on and around the East Mesa area. This program started with test plots in 1978 (Lathrop and Martin 1982) and then was expanded in coverage. Lawrence (1966) and Lubina (1978) found that grassland rodent species increased in number after fire in California chaparral. Blankenship (1982), working in pine forest on East Mesa, did not find this pattern.

Possible experimental errors should also be considered in evaluating the two East Mesa coyote diets. Four such factors relating to the proportion of a prey item in scats are presented. First, Bowyer et al. (1983) recorded a high frequency of vegetation in scats. Andelt and Andelt (1984) found that the proportion of indigestible material in a meal influenced the defecation rate of the coyote; when coyote eat vegetation the number of scats produced is higher per biomass intake. Second, remains of a single mammal prey (depending on size) may end up in more than one coyote scat (Weaver and Hoffman 1979). As a result, frequency data of mammal prey in scats cannot be directly equated with number of prey individuals. I did not collect droppings under 20 mm in diameter which should bias my sample towards larger prey since they lead to larger diameter coyote scat (Danner and Dodd 1982). Third, the estimated density of coyote in the Laguna Mountain area (Gould, pers. comm.) would predict about 6 individuals on East Mesa; coyote may produce 6 scats a day (Fichter et al. 1955). Based on these two values, both East Mesa coyote studies sampled less than 2% of the available coyote scats. These small samples may not be representative of the prey taken by coyote in the region. Finally, sample sizes of droppings per given time period was dissimilar for the two East Mesa studies and would influence the yearly proportion of prey items in the scats.

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Literature Cited

Andelt, W. F., and S. H. Andelt. 1984. Diet bias in scat deposition-rate surveys of coyote density. Wildl. Soc. Bull. 12(1):74–77.

Barrows, C. 1980. Feeding ecology of the spotted owl in California. Raptor Research 14(3):73–78.

Bekoff, M. 1977. *Canis latrans.* Mammalian Species 79:1–9, Amer. Soc. Mammal.

Blankenship, D. J. 1982. Influence of prescribed burning on small mammals in Cuyamaca Rancho State Park, California. P. 587 *in* C. E. Conrad and W. C. Oechel (Tech. Coords.). Proceeds. Symp. Dynamics and Manage. Mediterranean-Type Ecosys. U.S. For. Serv. Gen. Tech. Rept. PSW-58. 637 pp.

Bowyer, R. T. and V. C. Bleich. 1980. Ecological relationships between southern mule deer and California black oak. Pp. 292–296 *in* T. R. Plumb (Tech. Coord.). Symp. Ecol., Manage. and Util. of Calif. Oaks. U.S. For. Serv. Gen. Tech. Rep. PSW-44. 368 pp.

———, S. A. McKenna, and M. E. Shea. 1983. Seasonal changes in coyote food habits as determined by fecal analysis. Amer. Midl. Natur. 109(2):266–273.

Calif. Dept. Fish and Game. No date. Beaver Transplanting. Final report, Project California 18-D-2. Mimeo.

Danner, D. A. and N. Dodd. 1982. Comparison of coyote and gray fox scat diameters. J. Wildl. Manage. 46(1):240–241.

Ferrel, C. M., H. L. Leach, and D. F. Tillotson. 1953. Food habits of the coyote in California. Calif. Fish and Game 39(3):301–341.

Fichter, E., G. Schildman, and J. H. Sather. 1955. Some feeding patterns of coyotes in Nebraska. Ecol. Monogr. 25(1):1–37.

Gianini, C. A. 1935. Cougar and coyote. J. Mammal. 16(3):229.

Hawthorne, V. M. 1972. Coyote food habits in Sagehen Creek Basin, northeastern California. Calif. Fish and Game, 58(1):4–12.

Hilton, H. and N. P. Kutscha. 1978. Distinguishing characteristics of the hairs of eastern coyote, domestic dog, red fox and bobcat in Maine. Amer. Midl. Natur. 100(2):223–227.

Lathrop, E. W. and B. D. Martin. 1982. Response of understory vegetation to prescribed burning in yellow pine forests of Cuyamaca Rancho State Park, California. Aliso 10(2):329–343.

Lawrence, G. E. 1966. Ecology of vertebrate animals in relation to chaparral fire in the Sierra Nevada foothills. Ecol. 47(2):278–291.

Lubina, J. A. 1978. The effects of fire on rodent populations in the chaparral of southern California: a comparative approach. M.S. Thesis, Calif. State Univ., Long Beach.

MacCracken, J. G. 1981. Coyote foods in southwestern Colorado. Southw. Nat. 26(3):317–318.

Mayer, W. V. 1952. The hair of California mammals with keys to the dorsal guard hairs of California mammals. Amer. Midl. Natur. 48(2):480–512.

Moore, T. D., L. E. Spence, and C. E. Dugnolle. 1974. Identification of the Dorsal Guard Hairs of Some Mammals of Wyoming. Wyo. Game and Fish Dept. Bull. 14, Cheyenne.

Murie, A. 1940. Ecology of the coyote in the Yellowstone. Fauna of the Natl. Parks of the U.S. Cons. Bull. No. 4.

Pearson, O. P. 1966. The prey of carnivores during one cycle of mouse abundance. J. Anim. Ecol. 35(2):217–233.

Rathbun, A. P., M. C. Wells, and M. Bekoff. 1980. Cooperative predation by coyotes on badgers. J. Mammal. 61(2):375–376.

Stains, H. J. 1958. Field key to guard hair of middle western furbearers. J. Wildl. Manage. 22(1): 95–97.

Tappe, D. T. 1942. The status of beavers in California. Calif. Dept. Fish and Game Bull. 3.

U.S. Dept. Commerce. 1973–1983. Climatological Data, Annual Summary(ies), California. N.O.A.A. VOLS. 77-87, Nos. 13.

Weaver, J. L. 1980. Influence of food supply on coyote populations in Jackson Hole, Wyo. Pp. 185–226 *in* Proceeds. Second Conf. Sci. Res. Natl. Parks, Vol. 12: Terrestrial Biology: Zoology. U. S. Dept. Interior Rpt. NPS/ST-80/02-12. 411 pp.

———, and S. W. Hoffman. 1979. Differential detectability of rodents in coyote scats. J. Wildl. Manage. 43(3):783–786.

Weintraub, J. D. and G. Shockley. 1980. Use of incisors to identify genera in owl pellets. Bull. S. Calif. Acad. Sci. 79(3):127–129.

Wells, H. and J. L. King. 1980. A general "exact test" for N × M contingency tables. Bull. S. Calif. Acad. Sci. 79(2):65–77.

Whiteman, E. E. 1940. Habits and pelage changes in captive coyotes. J. Mammal. 21(4):435–438.

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The Influence of Mima Mounds on Vegetation Patterns in the Tijuana Estuary Salt Marsh, San Diego County, California

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Abstract.—Mima-type earth mounds, up to 18.6 m in diameter, occur in marsh, transition, and upland areas of the Tijuana Estuary, but are best developed at intermediate tidal elevations. Plant dominants on mounds grade from low marsh to upland species. Upland and high marsh species show steeper species-area relationships than low marsh species, reflecting insular patch dynamics. Mounds are activity centers for several herbivorous mammals that probably influence mound and intermound vegetation. The mounds create a highly patchy transition, and indicate that landward limits of marsh species are more reliable marsh boundary indicators than seaward limits of upland species.

Mima-type earth mounds, attributed to the long-term soil translocation activities of geomyid pocket gophers, occur in many locations in western North America (Cox 1984a). These mounds, which reach 2 m in height, 40 or more m in diameter, and 50 or more ha^{-1} in density, seem to be restricted to areas of original grassland habitat, including lower alpine tundra and areas transitional to desert scrub and salt marsh (Cox *in press*).

A survey of Mima mound distribution in San Diego County, in the southwestern corner of California, revealed mounds at several locations bordering the Tijuana Estuary salt marsh (Cox 1984b). This marsh has been studied extensively by Zedler (1977, 1982), Zedler et al. (1980), and Winfield (1980), but the marsh-upland transition has not been described. The salt marsh is relatively undisturbed and species-rich, while the transition zone from marsh to upland is heavily disturbed. The mounds, concentrated in the marsh-upland transition, are conspicuously different in their vegetation from intermound areas, and show extensive tunneling and digging by mammals. Elsewhere in California, Brown (1951) noted Mima mounds in the transition zone and upper salt marsh of San Francisco Bay near Port Chicago and Pittsburgh, Contra Costa County. Along the Gulf Coast of Louisiana and Texas, Mima-type mounds border salt marshes along the inner side of coastal sounds (Dietz 1945, Price 1949).

The presence of these mounds at the Tijuana Estuary provided an opportunity to examine questions relating to the influence of topographic heterogeneity on salt marsh vegetation, and to the mechanism of Mima mound formation. Previously, the transition from salt marsh to upland has been assumed to be a vegetational continuum along a simple environmental gradient (Harvey et al. 1978, Eilers et al. 1983). Mounds within the marsh-upland transition modify salinity and moisture relationships and create islands of habitat suitable for upland

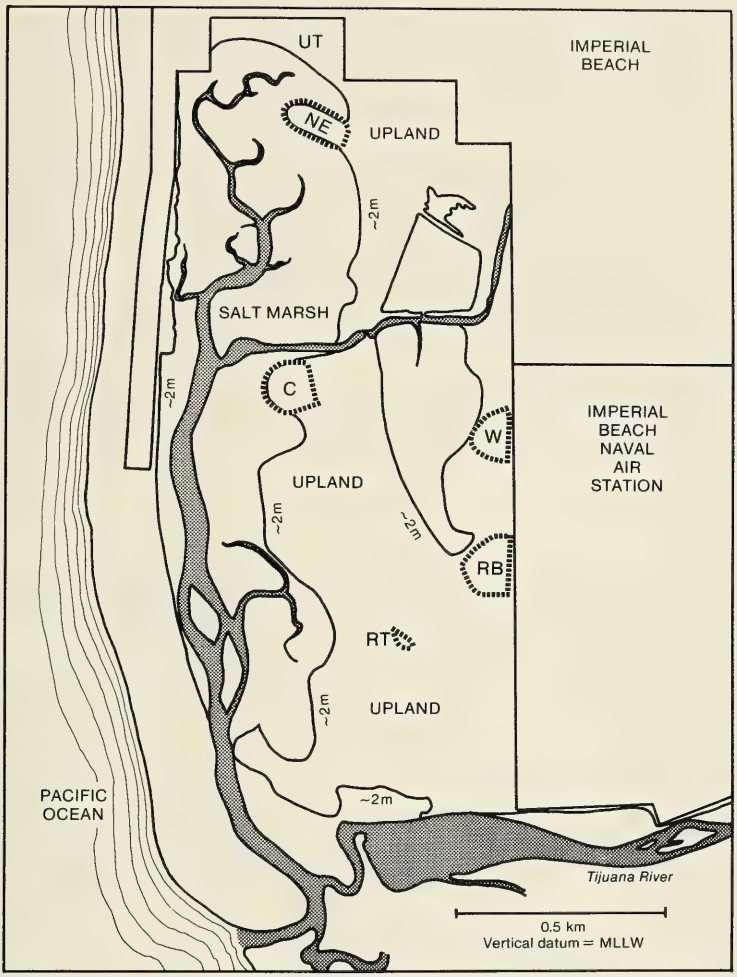

Fig. 1. Map of the Tijuana Estuary, San Diego County, California, showing Mima mounds fields examined in this study. The approximate 2 m MLLW contour is shown within the estuary. Study plots are coded as follows: NE—North End, W—Wheels, RB—Reed Bed, C—Central, RT—Ridge Top. The symbol *UT* designates the marsh-to-upland transition area that was examined but not sampled quantitatively.

plants and animals. Invasion of such areas of habitat by upland plants and by herbivorous mammals that utilize both upland and marsh plants may greatly complicate wetland boundary determination. Defining ecologically valid criteria for salt marsh boundaries is a matter of current major concern (Zedler and Cox 1985).

The origin of Mima mounds in Southern California has been the object of several physical and biotic hypotheses, but Cox (1984b) has strongly supported the hypothesis of their origin by the long-term process of soil translocation by geomyid pocket gophers. Under this hypothesis, maximum mound development should occur on soils of intermediate depth above a basement layer that causes frequent soil waterlogging and gives an advantage to animals living in spots of

elevated, well drained soils created by such translocation (Gakahu and Cox 1984). Thus, we hypothesized that the Tijuana Estuary mounds should show evidence of pocket gopher occupation, and should exhibit maximum size at an intermediate point in the marsh-upland transition, where their influence on vegetational features might be greatest.

Our studies were therefore designed to answer the following specific questions:

1. What is the extent of the mounded zone, and the pattern of heights, diameters, and spacing of the mounds?
2. How do soil salinity and other substrate conditions important to plant establishment and growth vary with mound size and location?
3. How are distribution and diversity of marsh and non-marsh plants related to mound size and location?
4. Are the floras of non-marsh species on mounds influenced by insular colonization and extinction processes?

Procedure

Study Area

The Tijuana Estuary (32°34′N, 117°7′W) lies just north of the Mexican Border at the mouth of the Tijuana River (an intermittent stream). The estuary (432 ha) includes about 166 ha of intertidal marshland and 164 ha of transition zone habitat (McIllwee 1970). Although the estuary has a long record of good tidal flushing (Zedler 1982), the ocean entrance became blocked during our study. The estuary proper then became hyposaline due to freshwater inflow from the Tijuana River, and later hypersaline due to evaporation during the dry summer and early autumn. The transition zone and upland habitat have been disturbed heavily by excavation and filling, construction of dikes and channels, and vehicle activity.

The Tijuana Estuary salt marsh has the richest flora of vascular halophytes of the 23 major southern California coastal wetlands (Zedler 1982). In common with other marshes that have experienced regular tidal flushing, the lowest marsh levels are dominated by cordgrass (*Spartina foliosa*). At higher levels, the marsh dominants are succulents, primarily pickleweed and glasswort (*Salicornia virginica* and *S. subterminalis,* respectively), and low, perennial, halophytic grasses (saltgrass, *Distichlis spicata*; shoregrass, *Monanthochloe littoralis*). In the transition zone, halophytes gradually give way to a variety of herbaceous plants (many of which are annual Mediterranean exotics), cacti, semi-woody subshrubs, and evergreen woody shrubs typical of California annual grassland and coastal sage scrub communities.

Methods

Mounds occur in five distinct locations in the northern and northeastern portion of the estuary (Fig. 1). In each location a plot spanning the available elevational range was selected and the mounds present were marked with numbered stakes. These mound groups were the main source of data for this study, but general observations were also made at several other locations. Mounds were present, for example, along most of the western side of the central ridge which separated the inner and outer marsh areas, and on which the Central plot was located (Fig. 1).

The physical and biotic characteristics of 86 mounds were assessed between 12

and 23 April 1984. Mound top and edge elevations were surveyed with a Wild Automatic Level; elevations were referenced to U.S. Army Corps of Engineers benchmark TJE-35, located at 2.03 m (6.58 ft) above Mean Lower Low Water (MLLW). Mound heights were obtained as the difference between top and edge elevations. Distance and direction from a single survey point in each area were also recorded to map each mound field. The maximum and minimum diameters of each mound and the distance to its nearest neighbor (center to center) were measured. Vegetational characteristics and the area of surface disturbed by animal digging were evaluated on a six-point cover scale: <1%, 1–5%, 5–25%, 25–50%, 50–75%, 75–100%. The percent coverage for each vacular plant species with live tissue or tissue produced during the 1983–84 winter growing season was estimated for each mound and for an equal-area intermound circle adjacent to, and at the same elevation as, the mound base. The areas of bare soil surface and of flotsam coverage were estimated in the same way. The probable animal agent responsible for any digging or tunneling was also noted.

Soil samples were collected from the top and base of 53 mounds in three locations (North End, Wheels, Reed Bed) on 17 June 1984. At this time the estuary entrance was closed, and river inflow had become impounded. On this date mounds at the lowest elevations (below about 1.95 m MLLW) were completely above water level, although they had been surrounded by shallow water (<10 cm deep) with a salinity of 15 parts per thousand during the April sampling period. Soil samples for 29 mounds in the Central area were collected on 14 September 1984, after the impounded water had receded. At this later date the estuary entrance was also closed, but re-entry of sea water had occurred and evaporation had caused water level to drop well below (about 54 cm) the basal elevation of the lowest mounds.

Soil salinities were measured as the electrical conductivity of uniform soil pastes, using a Lab-line Mark IV Mho-meter and the procedure outlined by Richards (1954).

Techniques of statistical analysis follow Zar (1984). Most correlation and regression analyses were performed only on mound data from North End, Wheels, Reed Bed, and Central areas, which overlapped in elevation. The four Ridge Top mounds were more than a meter disjunct in elevation. Plant nomenclature follows Munz (1974).

Results

Extent and Internal Geometry of Mounded Areas

The four mound areas in the upper marsh and transition zone (Fig. 1) ranged in size from 0.79 to 1.59 ha, and contained 15–29 mounds each (Table 1). Basal elevations of the mounds in these areas ranged from 1.87 to 2.88 m MLLW (Table 1). Mounds with basal elevations below 2.31 m MLLW are surrounded by water at regular high tides; those below 2.93 m MLLW are occasionally surrounded by storm tides. The lowest basal elevations in the Wheels and Reed Bed areas were 15–21 cm above those for the North End and Central areas. Of these four areas, Central showed the least evidence of disturbance by vehicle and foot traffic.

The Ridge Top area (Fig. 1) was less than 0.1 ha in area and lay at an elevation of 4.29–4.51 m MLLW (Table 1). The vegetation and soils of this small site

Table 1. Characteristics of Mima-type mounds and moundfields at the Tijuana River National Estuarine Sanctuary, San Diego County, California.

Mound group	Area (Ha)	Number of mounds	Range of basal elevations (m above MLLW)	Range of heights (m)	Range of diameters (m)	Mean distance to nearest neighbor (m ± SD)	Clark-Evans dispersion coefficient, R
North End	0.79	15	1.87–2.36	0.14–0.43	5.60–14.75	14.03 ± 2.92	1.22 ns*
Wheels	0.89	17	2.06–2.88	0.09–0.57	6.00–18.65	13.35 ± 2.06	1.16 ns
Reed Bed	1.59	21	2.08–2.63	0.10–0.44	6.10–18.45	14.98 ± 3.81	1.09 ns
Central	1.15	29	1.91–2.39	0.08–0.45	5.60–13.45	12.64 ± 3.01	1.27 $P < 0.01$
Ridge Top	0.09	4	4.29–4.51	0.14–0.27	8.00–11.40	9.55 ± 2.14	1.28 ns
Total	4.51	86	1.87–4.51	0.08–0.57	5.60–18.65	13.45 ± 3.24	1.17 $P < 0.01$

* R considered not significant (ns) at $P > 0.05$.

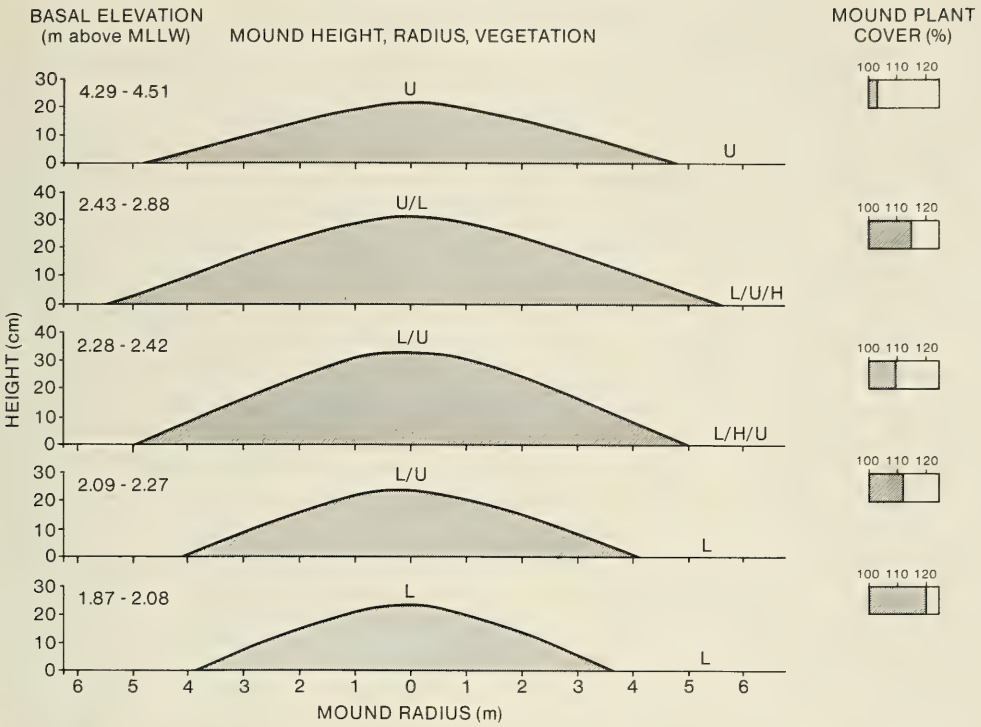

Fig. 2. Mound size and form, mound and intermound vegetation composition, and percent plant cover of Mima mounds in different elevational belts at the Tijuana Estuary, San Diego County, California. Symbols designate species categories: L—low marsh, H—high marsh, U—upland; categories are shown in decreasing order of total cover from left to right for mound and adjacent intermound areas.

suggested, however, that it was a relatively undisturbed remnant of the original upland habitat.

In the marsh and transition zone, mound heights and diameters varied with elevation (Fig. 2). Mound height increased significantly with elevation between 1.87 and 2.35 m MLLW ($r = 0.43$, $df = 50$, $t = 3.36$, $P < 0.001$). Between 2.32 and 4.51 m MLLW, however, mound height declined significantly with increasing elevation ($r = -0.332$, $df = 39$, $t = 2.20$, $P < 0.05$). The tallest mounds ($n = 11$), exceeding 0.4 m in height, all occurred between 2.28 and 2.62 m MLLW. The broadest mounds, exceeding 13 m in diameter ($n = 10$), spanned a wider elevational range, 2.18–2.84 m MLLW. Mound diameter was significantly correlated with elevation above MLLW ($r = 0.44$, $df = 80$, $t = 4.37$, $P < 0.001$). Mound height and diameter showed a significant correlation, as well ($r = 0.35$, $df = 80$, $t = 3.36$, $P < 0.01$). The regression equation for mound diameter (Y) as a function of height (X) was:

$$Y = 6.76 + 9.29X. \quad (1)$$

Analysis of mound spacing, using the technique of Clark and Evans (1954), indicated that the pattern tended to deviate from random in the direction of uniformity, the coefficient R exceeding 1.0 (Table 1). This deviation was signif-

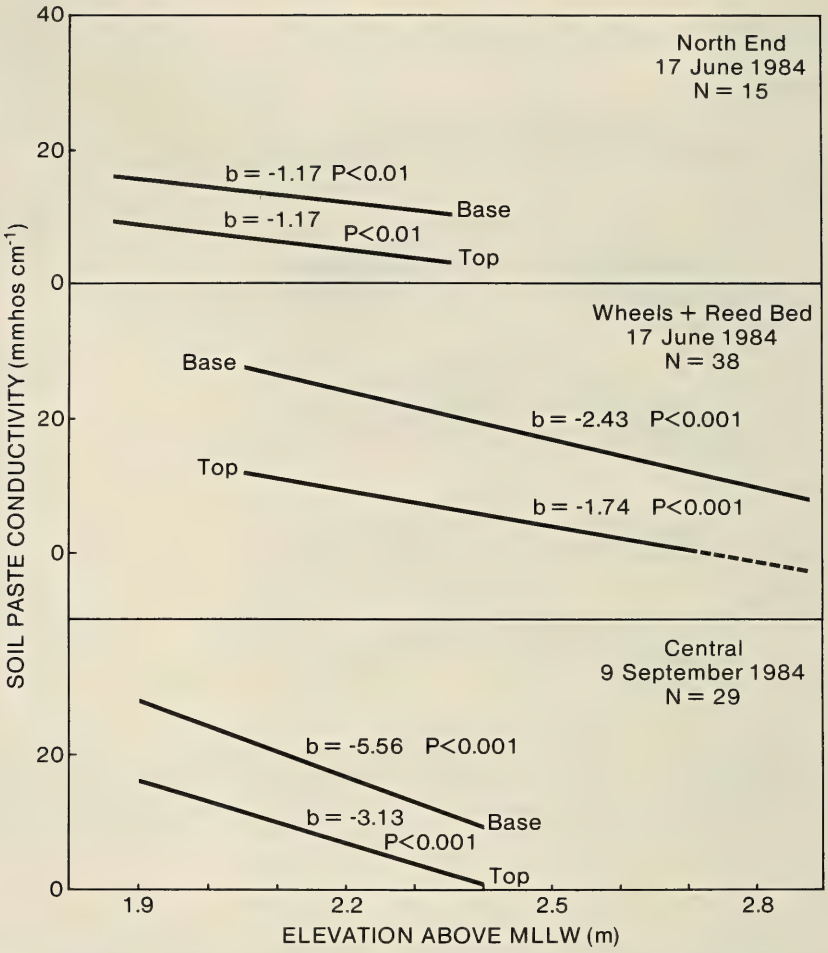

Fig. 3. Regression lines for mound top and mound edge soil salinities on elevation above Mean Lower Low Water for mound fields at the Tijuana Estuary, San Diego County, California.

icant, however, only for the Central area, the least disturbed mound group, and for all mound areas taken together. No significant relation existed between elevation above MLLW and distance to nearest neighbor.

Soil Salinity and Soil Disturbance by Animals

Soil salinity, expressed as the electrical conductivity of the soil paste, was higher for mound edges than for mound tops in all cases (n = 82). Salinity decreased with increasing height above MLLW (Fig. 3), but patterns differed for different mound areas. In areas sampled in June, 1984 (North End, Wheels, Reed Bed), salinities at mound edges were significantly higher than those on mound tops (North End: $t = 6.78$, $df = 27$, $P < 0.001$. Wheels and Reed Bed: $t = 14.46$, $df = 73$, $P < 0.001$). The patterns of change of mound top and mound edge salinity with elevation also did not differ between these two areas. However, salinities for the Wheels and Reed Bed areas were significantly higher than those for North End (Tops: $t = 5.35$, $df = 50$, $P < 0.001$. Edges: $t = 20.38$, $df = 50$, $P < 0.001$).

For the Central area, sampled later in the year, salinity showed a steeper relationship with elevation for mound tops than for mound edges ($t = 2.11$, $df = 54$, $P < 0.05$). In addition, the relation for mound base salinity and elevation for the Central area was significantly steeper than that for the North End area ($t = 2.91$, $df = 40$, $P < 0.01$), which was similar in its general position within the estuary system (Fig. 1). Mound height was also inversely correlated with mound top salinity ($r = -0.40$, $df = 80$, $t = 3.95$, $P < 0.001$).

Digging activity or tunneling by various animals was noted on all but 19 of 82 mounds in the marsh and transition zone. Surface heaps of the valley pocket gopher (*Thomomys bottae*) were found on 17 of 82 mounds, all with basal elevations over 2.08 m MLLW. In all but one case, a mound in the Wheels area with a basal elevation of 2.71 m MLLW, these heaps were many months old and appeared to have been flooded. Burrow systems of the California ground squirrel (*Spermophilus beecheyi*) were noted on 40 of 82 mounds, some as low as 1.90 m MLLW. Of these, 27 showed signs of very recent tunneling. Digging by dogs was noted on 12 mounds, usually in association with burrows of ground squirrels. One mound contained a burrow occupied by a striped skunk (*Mephitis mephitis*).

The extent of surface disturbance by digging (mid-point of percent cover class) by all animals together increased significantly with mound height ($r = 0.31$, $df = 80$, $t = 2.88$, $P < 0.01$). The area of bare soil, due both to digging and other factors, also increased significantly with increasing mound height ($r = 0.35$, $df = 80$, $t = 3.38$, $P < 0.001$) and also with increasing elevation above MLLW ($r = 0.32$, $df = 80$, $t = 3.07$, $P < 0.01$).

Distribution of Mound and Intermound Plants

In the marsh and transition zones, 34 species of vascular plants were recorded on mounds (Fig. 4); 2 additional species, *Spergularia villosa* and *Gasoul nodiflorum,* were found in the intermound areas sampled. Of the former, 11 were low marsh species with distributions extending below the elevations sampled, and 23 were high marsh or upland species whose lower limits occurred within the elevational range sampled. We sought prominent distributional breaks where several (3–5) species reached their upper or lower limits, and noted these at 2.08–2.09, 2.27–2.28, and 2.42–2.43 m MLLW (Fig. 4). In the Ridge Top area, which was over 4 m MLLW, 6 additional vascular plant species were encountered (Table 2). Only one high marsh species, of minor importance, occurred at this location.

Below 2.08 m MLLW, plant cover consisted mainly of low marsh species (Table 2, Fig. 2), most of which were non-succulents (Table 3). From 2.09 to 2.27 m marsh succulents increased in cover and succulents of upland affinity became prominent (Table 3). Between 2.28 and 2.42 m MLLW several other high marsh and upland forbs and grasses appeared, along with three species of cacti and other succulents, two coastal sage scrub subshrubs, and the perennial bunchgrass *Sporobolus airoides* (Table 2, Fig. 2). Over 77% coverage by succulent species was recorded in this zone (Table 3). Several of the typical low marsh species disappeared, as well. Above 2.43 m MLLW in the transition zone, a number of additional upland species appeared, notably the evergreen shrub *Rhus integrifolia.* Plant cover at this elevation was still dominated by the glasswort, *Salicornia subterminalis,* but the subshrub *Eriogonum fasciculatum* and the perennial bunchgrass *S. airoides* reached their maximum abundance here. The mounds of the

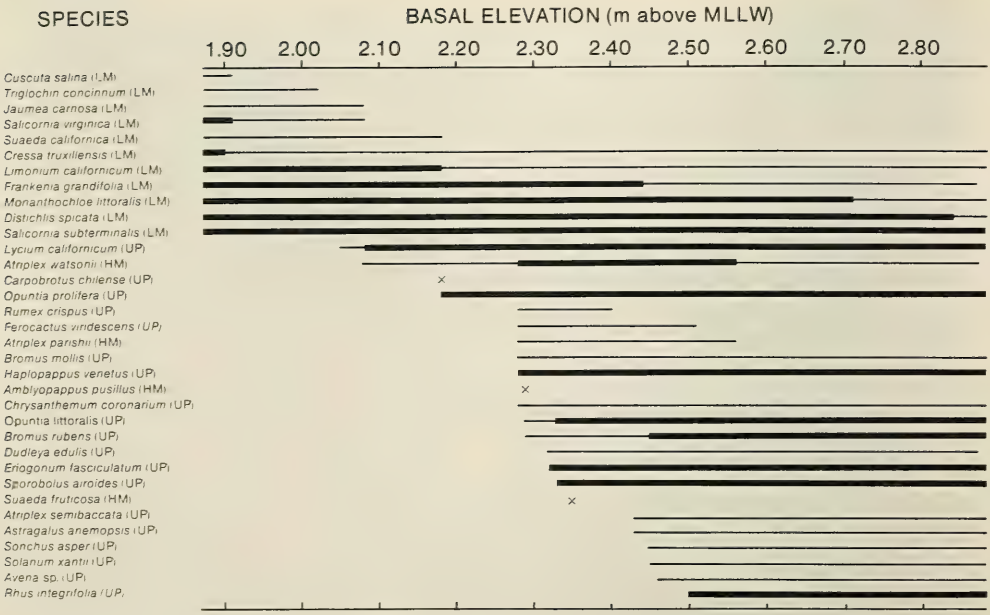

Fig. 4. Elevational ranges above Mean Lower Low Water for plant species occurring on Mima mounds at the Tijuana Estuary, San Diego County, California.

Ridge Top area, separated from other areas by an elevational gap of 1.41 m, were dominated by the woody evergreen shrub *Malosma laurina* and by coastal sage subshrubs (Tables 2, 3).

A small area spanning the elevational gap from transition zone to upland was located at the extreme north end of the estuary, near the North End mound group (Fig. 1, *UT*). Eleven mounds were present at this location, but they exhibited such extensive disturbance that no quantitative sampling was attempted. The dominant plants on these mounds were the woody evergreen shrubs *Rhus integrifolia* and *Simmondsia chinensis* (5 mounds), *Malosma laurina* and *S. chinensis* (5 mounds) and all three of these species together with *Atriplex canescens* (1 mound). Intermound areas here contained a scattering of marsh species at the lowest levels and a variety of coastal sage subshrubs and annual grasses and forbs at higher levels. Active pocket gopher digging was evident at this location.

Mean total plant cover on mounds was greatest in the lowest marsh zone and second greatest in the uppermost part of the transition zone (Table 2, Fig. 2). Mean cover was lower in the intermediate parts of the transition zone, where succulents reached their maximum abundance, and least on the upland site where marsh species were absent. Total plant cover for individual mounds bore a significant, but rather weak, direct correlation with mound area ($r = 0.28$, $df = 80$, $t = 2.56$, $P < 0.05$).

Similarity of mound vegetation to that of the adjacent intermound areas was determined by computing the coefficient of community, *C*, using mid-range values of percent cover classes for each species, by the equation

$$C = 2S/A + B, \quad (2)$$

Table 2. Mean percent cover of low marsh (LM), high marsh (HM), and upland (UP) plant species on Mima mounds at the Tijuana River National Estuarine Sanctuary in relation to elevation in meters above MLLW. Total cover is the sum of cover values for individual species, and includes overlap.

Species	Elevation above MLLW (m)				
	1.87–2.08 N = 21	2.09–2.27 N = 14	2.28–2.42 N = 23	2.43–2.88 N = 24	4.29–4.51 N = 4
Triglochin concinnum (LM)	0.02				
Cuscuta salina (LM)	0.02				
Salicornia virginica (LM)	0.83				
Suaeda californica (LM)	0.93	0.04			
Jaumea carnosa (LM)	0.31		0.02		
Monanthochloe littoralis (LM)	60.36	45.75	6.30	3.96	
Frankenia grandifolia (LM)	25.71	5.25	5.15	2.42	
Cressa truxillensis (LM)	1.26	0.28	0.17	0.81	
Limonium californicum (LM)	0.64	1.46	0.41	0.98	
Salicornia subterminalis (LM)	27.76	47.14	56.76	34.92	
Distichlis spicata (LM)	1.17	0.82	10.30	11.73	
Carpobrotus edulis (HM)		0.04			
Lycium californicum (UP)	0.88	9.54	15.85	13.38	
Atriplex watsonii (HM)	0.17	0.46	1.93	3.68	
Opuntia prolifera (UP)		1.28	3.91	6.67	
Opuntia littoralis (UP)			0.78		
Suaeda fruticosa (HM)			0.02		
Rumex crispus (UP)			0.20		
Amblyopappus pusillus (HM)			0.04		
Chrysanthemum coronarium (UP)			0.02		
Bromus mollis (UP)			0.04	0.27	
Bromus rubens (UP)			0.22	3.73	
Dudleya edulis (UP)			0.02	0.33	
Atriplex parishii (HM)			0.28	0.06	
Ferocactus viridescens (UP)			0.04	0.04	
Haplopappus venetus (UP)			3.30	7.44	0.88
Eriogonum fasciculatum (UP)			2.28	18.12	15.00
Sporobolus airoides (UP)			1.63	5.73	0.38
Rhus integrifolia (UP)				0.62	
Sonchus asper (UP)				0.02	
Solanum xantii (UP)				0.02	
Avena sp. (UP)				0.02	
Astragalus anemopsis (UP)				0.06	0.25
Atriplex semibaccata (UP)				0.44	0.12
Rhus laurina (UP)					56.25
Artemisia californica (UP)					26.20
Mirabilis laevis (UP)					3.00
Yucca schidigera (UP)					0.75
Lotus scoparius (UP)					0.12
Limonium sinuatum (HM)					0.12
Total	120.06	112.06	109.67	115.45	103.07

where S is the sum of shared percentages for species in common, and A and B are the sums of percentages for all species of the mound and intermound areas, respectively. Similarity values ranged from 0.06 to 0.98, and showed a significant negative relationship with mound area ($r = -0.31$, $df = 80$, $t = 2.92$, $P < 0.01$).

Table 3. Mean percent cover of major life form groupings of vascular plants on Mima mounds at the Tijuana River National Estuarine Sanctuary in relation to elevation in meters above MLLW.

Life form group	Height above MLLW				
	1.87–2.08	2.09–2.27	2.28–2.42	2.43–2.88	4.29–4.51
Low marsh species					
Non-succulent monocots	61.55	46.57	16.60	15.69	
Non-succulent dicots	27.63	6.99	5.73	4.21	
Succulents	29.83	47.18	56.78	34.92	
High marsh/upland species					
Succulents	0.88	10.86	20.62	20.42	0.75
Non-succulent forbs	0.17	0.46	2.47	4.26	0.49
Annual grasses			0.26	4.02	
Perennial grasses			1.63	5.73	0.38
Coastal sage subshrubs			5.58	25.58	45.20
Evergreen woody shrubs				0.62	56.25
Total	120.60	112.06	109.67	115.45	103.07

Species-Area Relations of Mound and Intermound Plants

From 3 to 15 vascular plant species were recorded on mounds and 3 to 14 species in the adjacent intermound areas of same size. Within the marsh and transition zones, number of mound species increased significantly with elevation above MLLW ($r = 0.38$, $df = 80$, $t = 9.69$, $P < 0.001$) and with mound height ($r = 0.41$, $df = 80$, $t = 4.00$, $P < 0.001$). Combined in the following multiple regression equation, elevation in m above MLLW (X_1) and mound height (X_2) gave a multiple correlation coefficient (R) of 0.76 with number of mound species (S):

$$S = -13.02 + 8.66X_1 + 6.10X_2. \quad (3)$$

Distinctive species-area relationships existed for numbers (S) of mound and intermound species, as reflected in the coefficients of the power function,

$$S = bA^z, \quad (4)$$

in which A is mound area in m^2. The slope, z, of the species-area relationship was much steeper for mound than for intermound areas, differing little whether all species or only perennial species were considered (Table 4). The species-area slope was also much steeper for high marsh and upland species than for low marsh species (Table 4). Slope values for marsh species were not significantly different from 0. Because of the strong correlation of number of mound species with elevation above MLLW, the species-area relationship for high marsh and upland species was examined by a two-factor regression that related number of species to both area in m^2 (A) and elevation in m MLLW (X) by the equation,

$$\text{Log } S = \log b + z_1 \log A + z_2 \log X. \quad (5)$$

This analysis yielded the specific coefficients

$$\text{Log } S = -2.461 + 0.338 \log A + 6.138X, \quad (6)$$

which possessed a multiple correlation coefficient, R, of 0.78. In this equation, the slope, z, of the species-area relation was reduced to 0.338, which was still

Table 4. Coefficients of the species-area power function, $S = bA^z$, in which S is number of species and A area in m^2, for mound and intermound areas at the Tijuana Estuary, San Diego County, California.

	Mounds		Intermounds	
	b	z	b	z
All vascular plant species	0.077	0.453	0.422	0.246
Vascular perennials only	0.098	0.429	0.451	0.218
High marsh/upland species	−0.594	0.582	−0.327	0.391
Low marsh species	0.487	0.126	0.726	0.032

much steeper than for low marsh species on mounds. Efforts to incorporate other factors, such as the area of soil distubance by animal digging, into this equation gave no additional significant variables.

Discussion

Mima-type mounds at the Tijuana Estuary tend toward maximum development at an intermediate point in the marsh–upland transition, roughly between 2.2 and 2.8 m MLLW. Their dispersion shows a significant tendency toward uniformity, but spacing distance does not vary significantly with elevation above MLLW. This geometry is consistent with the hypothesis that these mounds are formed by geomyid pocket gophers and their spacing determined by the territorial behavior of these animals. Their maximum development at an intermediate position in the gradient matches the prediction of the pocket gopher hypothesis that mound growth will be most active under conditions of intermediate limitation of use of intermound soils by fossorial rodents (Gakahu and Cox 1984). At the lowest levels, the dense silty-clay marsh soil (Zedler et al. 1980) and frequent flooding severely limit the extent of tunneling into intermound areas when animals are present; periods of unusually high water also eliminate the animals from these mounds periodically. In the loamier, better drained soils of the upland areas, the advantages of nest location in areas of elevated soil are weaker, and the tendency for soil to be translocated consistently toward such spots much less. In the transition zone, however, flooding appears to be frequent enough to force animals to locate their permanent nest chambers in elevated areas, yet infrequent enough to allow extensive tunneling into surrounding lower areas, with a resultant strong displacement of soil moundward.

The critical factor limiting occupancy of mounds by upland species is probably soil salinity, which differed markedly between the tops and bases of even the lowest mounds. Neuenschwander et al. (1979) also found salinity to be the limiting factor for upland species at Bahia San Quintin, Baja California. The fact that Mima mounds create low salinity conditions and permit upland species to extend far beyond the point at which intermounds become dominated by marsh species means that the maximum limits of penetration of upland species cannot be used as a meaningful criterion for the boundary of this marsh area.

Several additional factors probably determine precisely which upland species are present on mounds, however. The high species-area slope for high marsh and upland species indicates that mound habitats are highly variable in the floras of these species in both space and time. Extinctions of these species are probably

frequent on smaller mounds, where they are also slow to be offset by seedling reestablishment. Low marsh species, on the other hand, show a very flat species-area relationship both for mound and intermound areas. The fact that low marsh species are mostly perennials that reproduce vegetatively (Neuenschwander et al. 1979, Zedler 1982) means that they are able to spread quickly and colonize suitable habitat. Their presence on mounds is probably due mostly to vegetative expansion from adjacent intermound areas.

The steep species-area relationships of high marsh and upland species (Table 4) probably reflect several factors. For intermounds, the steep relation ($z = 0.391$) presumably reflects only the effects of environmental instability on the establishment and survival of high marsh and upland species in a marginal habitat together with factors affecting the dispersal of their seeds from source areas at higher elevations. For mounds, the relationship probably reflects three additional factors: 1) differential elevational distribution of large and small mounds, 2) differential environmental stability of large and small mounds, and 3) differential establishment opportunities for plants on large and small mounds. The largest mounds occur at an intermediate elevation where conditions near the mound base favor low marsh species and those at the top high marsh and upland species; soil salinity is probably the most important of these conditions. Secondly, variations in water levels and salinity within the estuary, due to events such as winter rainfall, river flooding, storm tidal surges, and occlusion of the estuary mouth, create highly variable soil conditions, particularly on the smaller mounds that are most frequent at lower elevations above MLLW. Alternation of hypo- and hypersaline conditions may thus cause high turnover of species on small mounds, while the floras of large mounds are less severely affected. Finally, as suggested by the fact that a steep species-area relation was still shown for non-marsh mound species when elevation was taken into account (Equation 5), establishment of species on larger mounds is probably easier than on small mounds. The establishment of high marsh and upland species that reproduce by seed is probably favored on large mounds by the significantly greater percentages of bare soil and soil disturbed by animal digging, and their persistance by the larger areas of suitable habitat.

The overwhelming dominance of succulents on mounds at intermediate elevations (Table 3) suggests that these sites pose critical moisture challenges to both marsh and upland species. Total plant cover was lower in this elevational range than in other levels of the marsh-upland transition, perhaps as a reflection of this challenge.

Mounds appeared to provide optimal habitat for a number of non-marsh species that were largely absent from the nearby remnants of upland habitat. These included the succulents *Lycium californicum, Ferocactus viridescens,* and *Dudleya edulis.* Although all three of these species also occurred in intermound areas in the uppermost transition zone, the most robust, and presumably oldest, individuals were located on mounds. These species obviously possess a high degree of tolerance of desiccation stress, but their strong association with marsh mounds may also reflect the action of other factors that exclude them from nearby upland areas. One such factor, perhaps more important in the past than at present, is fire. All three species are absent from inland areas where fire is frequent, or are confined to rocky sites and cliffs where fire effects are weak or absent.

Mima-type mounds at the Tijuana Estuary are heavily utilized by herbivorous

mammals, including burrowing species such as the valley pocket gopher and California ground squirrel and nonburrowing species such as the Audubon's cottontail (*Sylvilagus auduboni*) and black-tailed jackrabbit (*Lepus californicus*), both of which maintain hiding places in the dense mound-top vegetation. Both the pocket gopher and ground squirrel were apparently eliminated from mounds in most of the transition zone and marsh proper by prolonged flooding during the winter of 1982–1983. The ground squirrel is rapidly recolonizing mounds far into the marsh, but recolonization by the pocket gopher will probably be slower because of the limited above-ground exploratory behavior of this species. Both cottontails and jackrabbits are abundant. The combined population of these herbivores is considerable, and their above- and below-ground browsing activities may influence the composition of the marsh vegetation in significant fashion. Neuenschwander et al. (1979) also noted that the transition zone at Bahia San Quintin, Baja California, received heavy use by upland animals.

The presence of *Sporobolus airoides* in mound and intermound sites at several locations in the Tijuana Estuary raises the question of the vegetation type that bordered the salt marsh in presettlement time. *S. airoides* forms several extensive patches in the Reed Bed mound area, and occurs on and between mounds at several locations on the ridge between eastern and western marsh areas. The present vegetation of upland areas that do not appear to have experienced excavation or filling is now annual grassland with a mixture of coastal sage species. The presence of this important perennial bunchgrass, a species typical of moderately saline or alkaline prairie soils throughout the western United States, suggests that the Tijuana Estuary may have been bordered by California Valley Grassland prior to European settlement.

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Literature Cited

Brown, H. C. 1951. Mound microrelief of the Columbia Plateau and adjacent areas. Unpublished manuscript.

Clark, P. J. and F. C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology, 35:445–453.

Cox, G. W. 1984a. Mounds of mystery. Natural History, 93(6):26–45.

———. 1984b. The distribution and origin of Mima mound grasslands in San Diego County, California. Ecology, 65:1397–1405.

———. *In press.* Mima mounds as an indicator of the presettlement grassland-chaparral boundary in San Diego County, California. American Midland Naturalist.

Dietz, R. S. 1945. The small mounds of the Gulf coastal plain. Science, 102:596–597.

Eilers, H. P., A. Taylor, and W. Sanville. 1983. Vegetative delineation of coastal salt marsh boundaries. Environmental Management, 7:443–452.

Gakahu, C. G. and G. W. Cox. 1984. The occurrence and origin of Mima mound terrain in Kenya. Afr. J. Ecol., 22:31–42.

Harvey, H. H., M. J. Kutilek, and K. M. DiVittorio. 1978. Determination of transition zone limits in coastal California wetlands. Unpublished report to the U.S. Environmental Protection Agency, Washington, D.C.

McIllwee, W. R. 1970. San Diego County coastal wetland inventory: Tijuana Slough. Unpublished report, California Fish and Game Department, Sacramento, CA.

Munz, P. A. 1974. A flora of southern California. Univ. of California Press, Berkeley, CA.

Neuenschwander, L. F., T. H. Thorstad, Jr., and R. J. Vogl. 1979. The salt marsh and transitional vegetation of Bahia San Quintin. Bull. S. Calif. Acad. Sci., 78:163–182.

Price, W. A. 1949. Pocket gophers as architects of Mima (pimple) mounds of the western United States. Texas J. Sci., 1:1–17.

Richards, L. A. (Ed.) 1954. Diagnosis and improvement of saline and alkali soils. USDA Agricultural Handbook No. 60, Washington, D.C.

Winfield, T. P. 1980. Dynamics of carbon and nitrogen in a southern California salt marsh. Ph.D. Dissertation, Univ. of California, Riverside and San Diego State University, San Diego, CA.

Zar, J. H. 1984. Biostatistical analysis. Second Ed. Prentice-Hall, Inc., Englewood Cliffs, NJ.

Zedler, J. B. 1977. Salt marsh community structure in the Tijuana Estuary, California. Estuarine and Coastal Marine Science, 5:39–53.

———. 1982. The ecology of southern California coastal salt marshes: a community profile. U.S. Fish and Wildlife Service, Biological Services Program, Washington, D.C. FWS/OBS-81/54. 110 pp.

———, and G. W. Cox. 1985. Characterizing wetland boundaries: a Pacific Coast example. Wetlands, 4:43–55.

———, T. Winfield, and P. Williams. 1980. Salt marsh productivity with natural and altered tidal circulation. Oecologia (Berl.), 44:236–240.

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Research Notes

Inter- and Intralocular Distribution of Yucca Moth Larvae in *Yucca whipplei* (Agavaceae)

Pollination of *Yucca* species is dependent upon the services of a moth in the genus *Tegeticula* (Trelease 1893). In this mutualistic relationship the moth is in turn dependent upon the flowers for oviposition sites. Previous studies have shown that the number of moth larvae, and consequently seed loss, are highly variable, among *Yucca* species (Keeley et al. 1984).

Yucca whipplei is a common species on shallow soils throughout the foothills of southern California and the southern Sierra Nevada. This species is distinct from other yuccas in that it is the only one with monocarpic reproduction, i.e., dying after reproduction, (at least in two of the five subspecies, see Haines 1941). In addition, while the majority of *Yucca* species are pollinated by *Tegeticula yuccasella, Y. whipplei* has a different species of moth (*T. maculata*) restricted to it. A recent study of yucca moth seed predation on *Yucca whipplei* (Keeley et al. 1986 press) has shown that the distribution of moth larvae is highly variable, among subspecies, among individuals within populations, and even among capsules within an inflorescence.

This variation prompted an investigation into the distribution of moth larvae within the fruits of *Yucca whipplei.* Two questions are addressed. 1) For fruits with more than a single moth larva, are the larvae randomly distributed among the six locules in the fruit? 2) Within a locule, are larvae randomly distributed along the length of the capsule?

Methods

Mature capsules were collected from plants throughout the range of *Yucca whipplei* (see Keeley et al. 1986 for localities). Capsules were opened and the relative distribution of larvae within capsules was indicated by numbering each of the six locules beginning with the first locule in which a larva was encountered and noting this number for each subsequent larva. Distribution of larvae within locules was described by measuring the distance from the base of the capsule to the nearest seed destroyed.

Results

To determine if multiple larvae within a capsule were randomly distributed between locules, the number of capsules with only two larvae were used to determine the proportion of larvae in the adjacent locule vs. nonadjacent locules. If larvae are randomly distributed in a capsule with six locules, the probability that a second larva would be adjacent to an occupied locule would be 2/5, and 3/5 that it would occur in a non-adjacent locule. The Chi-square test for goodness of fit showed no significant departure from expectation ($P > 0.05$, $N = 180$). Thus, moth larvae were randomly distributed among locules within a capsule.

The distribution of larvae within a single locule, however, was highly skewed.

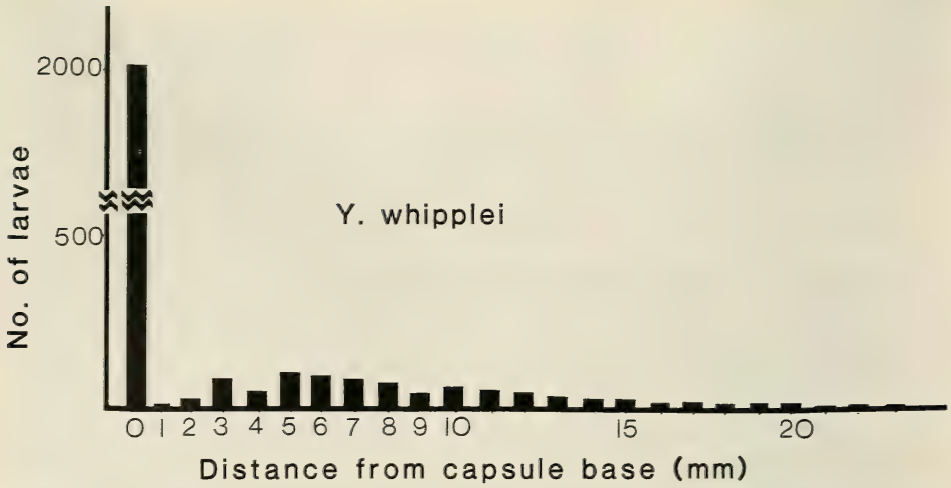

Fig. 1. Distribution of *Tegeticula maculata* larvae within locules of *Yucca whipplei* fruits (sample size: N = 2912 larvae).

The Chi-square tests for goodness of fit showed a highly significant departure from normality ($P < 0.01$). As seen in Fig. 1, the vast majority of moth larvae in *Yucca whipplei* fruits were situated at the base of the capsule.

Due to this very skewed distribution the question arose as to whether this was a characteristic of *Yucca* species in general. The intralocular distribution of larvae was determined from data collected previously (Keeley et al. 1984) for nine other *Yucca* species from the southwestern U.S. These included species with dehiscent capsular fruits (*Y. angustissima, Y. elata, Y. glauca, Y. reverchoni*) and species with indehiscent baccate fruits (*Y. baccata, Y. brevifolia, Y. schidigera, Y. schottii, Y. torreyi*). Fig. 2 shows the intralocular distribution of larvae for one of these

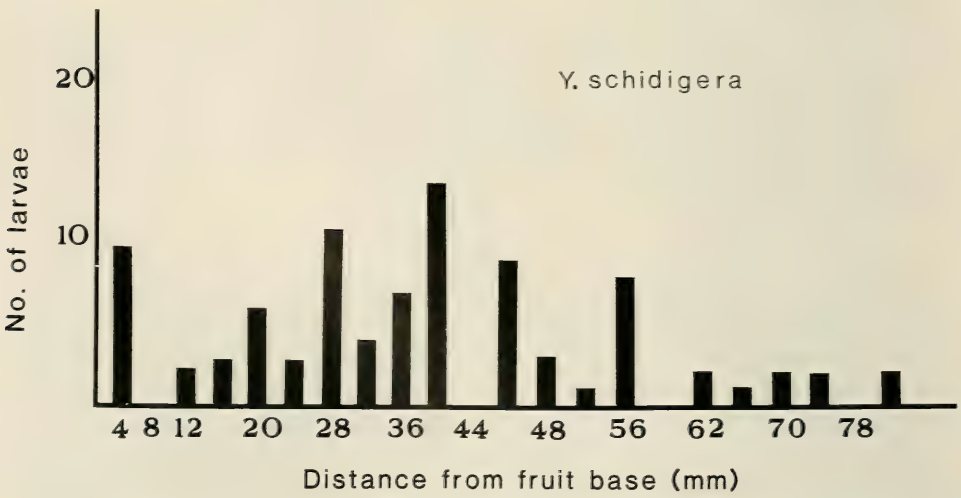

Fig. 2. Distribution of *Tegeticula yuccasella* larvae within locules of *Yucca schidigera* fruits (sample size: N = 82 larvae).

Fig. 3. Open capsules of *Yucca whipplei* illustrating the typical site of oviposition (point of constriction of the capsule), larval chamber (arrow) consisting of destroyed seeds glued together and most common position of the larval chamber within the capsule by Teresa Montygierd-Loyba.

species which closely resembles the pattern observed for the other eight species. For all nine of these species the distribution of larvae along the length of the capsule did not depart significantly from normality ($P > 0.05$).

Discussion

Particularly intriguing is the distribution of larvae within the locules of *Yucca whipplei* (Fig. 1). The highly skewed distribution of moth larvae in *Y. whipplei* capsules is in marked contrast to the intralocular distributions of the larvae in nine other *Yucca* species from the southwestern U.S. These other nine species represent most of the range of variation in the genus with respect to fruit characteristics.

There are characteristics unique to *Yucca whipplei* which could explain the highly skewed intralocular distribution of larvae in this species but not in others. For example differences in floral structure could affect oviposition location; in *Y. whipplei* flowers, the stamens tend to spread whereas in other yuccas they are erect or appressed to the carpel. Behavioural differences in oviposition site and/or orientation of larvae may be involved as *Y. whipplei* has a unique *Tegeticula* species. One characteristic of *T. maculata* that could be involved is the fact that the larvae of this species produce a silk that glues together the remains of the seeds they eat and thus forms a chamber (Fig. 3). Experiments have shown that if these chambers, rather than being situated at the base of the capsule, are artificially placed higher up, they act as a plug and block the dispersal of all seeds situated beneath them (A. Meyers and J. Keeley, unpublished data). This is due

to the fact that the upright capsules do not open completely and, due to a rudimentary false septum the seeds must escape upwards (McKelvey 1947). The positioning of larval chambers at the base of the capsules is apparently due to the orientation of the feeding larva since the female typically oviposits near the middle, as evidenced by direct observation (Trelease 1893) or presence of apparent oviposition scars (J. Keeley personal observation).

In other *Yucca* species the moth larvae may not create a seed dispersal problem for two reasons. In the baccate-fruited species the fruits are indehiscent and thus the position of the larvae should not have any effect on ultimate seed dispersal. In the other *Yucca* species with dehiscent capsules, the yucca moth (*Tegeticula yuccasella*) larvae are larger and do not produce a silk which binds the seed remains together into a chamber; thus less seed debris is left behind and since it is not glued together it disperses as well as or better than good seeds.

It is concluded that non-random orientation of moth larvae within the locules of *Yucca whipplei* fruits has been selected for as a means of enhancing the dispersal of seeds not consumed by the yucca moth.

Literature Cited

Haines, L. 1941. Variation in *Yucca whipplei.* Madrono, 6:33-45.

Keeley, J. E., S. C. Keeley, and D. A. Ikeda. 1986. Seed predation by yucca moths on semelparous, iteroparous, and vegetatively reproducing subspecies of *Yucca whipplei* (Agavaceae). Am. Midl. Nat., 115:1–9.

Keeley, J. E., S. C. Keeley, C. C. Swift, and J. Lee. 1984. Seed predation due to the Yucca-moth symbiosis. Am. Midl. Nat., 112:187–191.

McKelvey, S. D. 1947. Yuccas of southwestern United States, Pt. 2. Arn. Arbor., Harvard Univ., Jamaica Plain, Mass.

Trelease, W. 1893. Further studies of yuccas and their pollination. Ann. Rep. Mo. Bot. Gard., 4: 181–226.

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A Note on the Trigger Pollination Mechanism in the Camphor Weed (*Trichostema lanceolatum*) as Related to Pollinator Weight and Behavior

The camphor weed or vinegar weed (*Trichostema lanceolatum* Benth.) is one of the North American members of the mint family (Lamiaceae). The upper portion of its light blue corolla forms a thin tube which contains the anthers and style (Fig. 1A). When a foraging insect alights on the lower lobes of the corolla, and inserts its mouth parts into the nectar-containing lower section of the same tube, the narrow corolla portion above is straightened and snaps rapidly downward brushing pollen onto the back of the visiting insect (Fig. 1B). After the pollinating insect leaves, the narrow tube flips back up into its original position. This action has been previously described by T. Spira (1978) who attributed the trigger effect to the weight of the pollinating insect on the corolla lobes. In this note an attempt is made to determine if some insect behavior (in addition to its weight or even instead of its weight) may be responsible for flexing the tube in certain circumstances.

Relationships where a flower dusts pollen onto the dorsal surface of a visiting insect are called "nototribic" and are not uncommon in other species of the genus *Trichostema* as noted by T. Spira (1978, 1980) or other genera in the mint family—see Proctor and Yeo (1972) and L. W. Macior (1974). Although he described these and other features of camphor weed, T. Spira reported no study of this flower's action in response to weight or behavior of its pollinating species. Such data may be valuable in understanding the relationships between insects and pollination in this species and may shed light on the pollination process in other nototribic taxa as well.

In order to estimate the amount of pollinator weight alone required on the lower corolla lobes to trip the mechanism, the central lower lobe of the corolla was pierced with a staple, from which additional staples could then be hung. These were Bates Standard staples and each had a weight of 33 mg. From tests performed on 60 different *Trichostema lanceolatum* flowers in 1983 and 1984 the following was recorded: 23% of the 60 flowers were triggered by only one staple (33 mg), 58% by two staples (66 mg), and the remaining 19% by three staples (99 mg) so that all flowers tested required less than 99 mg to trigger their pollen apparati.

These data should be compared to the weights of the various bees and one of the moth species which according to Spira (1980) and Howe (1985) routinely visit the camphor weed flowers. Each insect was collected, stunned in an ethyl acetate jar, and then immediately weighed on a Sartorius balance. The mean weights and standard deviations for each species were as follows where n = 6: bumblebees (*Bombus sonorus* Say) 223 ± 21 mg, honey bees (*Apis mellifera* L.) 90 ± 4.5 mg, female mason bees (*Anthophora urbana* Cresson) 98.3 ± 13 mg, and the woodland skipper moth (*Ochlodes sylvanoides sylvanoides* Boisduval) 87.8 ± 7.2 mg.

Of the bees which regularly pollinate *T. lanceolatum,* Howe (1985), all *Bombus sonorus* individuals are obviously heavy enough to trigger this mechanism by weight alone. The honey bees, the female mason bees, and the woodland skipper

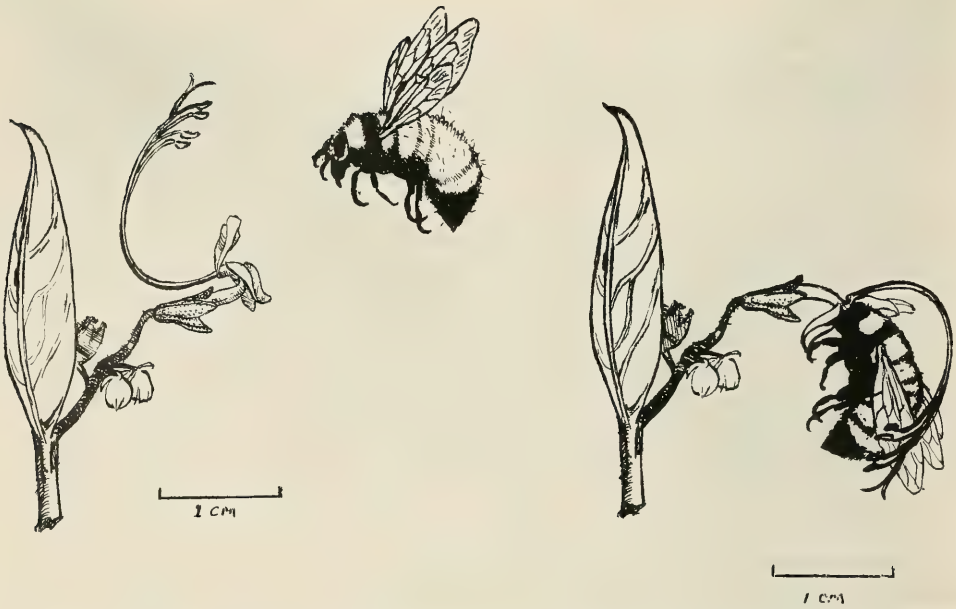

Fig. 1A. *Trichostema lanceolatum* (camphor weed) flower before the bumble bee (*Bombus sonorus*) has alighted in quest of nectar. Drawing by Ross Marshall. Fig. 1B. *T. lanceolatum* flowers after the bumble bee has landed. When the bee alights, the weight of its body and the action of its mouth parts in the floral tube cause the anthers and the style to flex rapidly downward, dusting the pollen onto the dorsal surface of the bee's abdomen. Drawing by Ross Marshall.

moths would also be able to flex most camphor weed flowers by their weight on the corolla lobes alone. The two mason bee males collected, however, had weights of only 59 and 53 mg respectively and were thus too light to have tripped many of the flowers tested. Since 23%–81% of the flowers were tripped with 1–2 staples, perhaps *some* flowers were tripped by weight and other heavier flowers are unavailable to mason bee males.

An attempt was made to see if a light insect such as these *A. urbana* males might be triggering the camphor weed flower mechanism by simply thrusting its mouth parts into the curved corolla—thereby mechanically straightening out the S-shaped upper tube. Upon intromission into the corolla tube, each of the following objects would routinely flex the flower tube without any weight on the lower corolla lobes: bristle of "soft" toothbrush, polyolefin bristle of two-inch paint brush, the mouth parts of honey bee heads held with tweezers. Since these objects can be used to flex the flower mechanism, it is possible that the action of insect mouth parts and/or tongues normally plays an important role in this process.

It has thus been shown that there is a close relationship between the force required to flex the pollinating apparatus of camphor weed and the actual weight of its key pollinating species. The weight of most of its pollinating insects is slightly greater than the minimum force required to spring the pollinating mechanism. While other workers have assumed that it is simply the weight of the pollinator that is solely responsible for flexing the corolla, it is shown here that some smaller insects might trigger the flower by thrusting their mouth parts into the corolla

tube and thereby supplying some or all of the force required to bend the pollinating tube of the flower.

Acknowledgments

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Literature Cited

Howe, G. 1985. A census of pollinator bees in large and small populations of the camphor weed (*Trichostema lanceolatum*). Crossosoma 11(2):1–7.

Macior, L. W. 1974. Behavioral aspects of coadaptations between flowers and insect pollinators. Ann. Mo. Bot. Gard. 61:760–769.

Proctor, M., and P. Yeo. 1972. The pollination of flowers. Taplinger Publ. Co., New York.

Spira, T. 1978. Floral parameters associated with breeding system and pollinator type in *Trichostema* (Labiatae). Master of Arts Thesis, Cal. State Univ. Chico.

———. 1980. Floral parameters, breeding system and pollinator type in *Trichostema* (Labiatae). Amer. J. Bot. 67(3):278–284.

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Some Observations of the Alpheid Shrimp *Betaeus setosus* Hart with Its Host, *Pachycheles rudis* Stimpson

Shrimps of the family Alpheidae are well known for their symbiotic relationships with other species of crustaceans, molluscs, echinoderms, or fish (Lassig 1977; Karplus et al. 1972; Ache and Davenport 1972). Along the west coast of North America, *Betaeus harfordi* is found in the mantle cavities of abalones (*Haliotus* spp.), while *B. macginitieae* occurs in pairs under sea urchins of the genus *Strongylocentrotus* and *B. harrimani* is associated with the burrows of the ghost shrimps *Callianassa* and *Upogebia* (Hart 1964).

Betaeus setosus, a small species ranging from British Columbia to central California, has been considered an outer coast species as it has not previously been recorded from sheltered waters in British Columbia or Washington (Butler 1980; Kozloff 1974). Collections made at several sites within Puget Sound, however, have shown that this species is fairly common in suitable habitats and is invariably associated with the anomuran crab *Pachycheles rudis.* Hart (1964) noted that *B. setosus* had been found in cavities under the holdfasts of kelp or eelgrass roots with *Pachycheles,* but considered the species to be free-living.

In Puget Sound, *Pachycheles rudis* is found in relatively high current areas, with male-female pairs frequently inhabiting empty giant barnacles (*Balanus nubilis*) or clinging to the underside of large rocks. In each case only one shrimp occurred with each pair of *Pachycheles,* where it was found lying on its side underneath the abdomen of one of the crabs.

In order to study this relationship, the shrimps and their hosts were placed in an aquarium in which sections of giant barnacle shells had been attached to the glass. A "blind" was made to allow close-up observations without disturbing the inhabitants. The *Betaeus* remained in constant contact with their hosts throughout the day and left the shells at night, possibly to forage. Shrimps were sometimes pushed away by their hosts upon returning to the shell, but would persist and eventually get under the crab from the side or behind. No apparent signals were visible in either the shrimp or the host crab, as have been reported for some tropical species (Vannini 1985; Karplus et al. 1972); however the hurried return of the shrimp (induced by artificial light) may differ from their return under natural lighting conditions. Once in position, even a great deal of movement on the part of the shrimp failed to elicit any visible response from the crab.

Betaeus setosus has been found in pairs (Hart 1964), however, the captive specimens were quite territorial and would not tolerate another specimen in their shell. The large chelipeds were used to push other shrimps away, but in no case were they used to pinch the intruder. Unfortunately, the sexes of the specimens involved in these encounters was not known. *Betaeus* was never observed feeding inside the shells; it is suspected that the primary advantage of the relationship is one of protection for the shrimp, and that feeding is done outside the shell at night. *Pachycheles* is strictly a filter feeder and herbivore and represents no threat to *Betaeus,* while its large, powerful chelae may effectively discourage predators.

Whether *Pachycheles* derives any benefit from this relationship or merely tolerates it is not yet known.

Betaeus harfordi has been demonstrated to locate its host by chemosensory means, while *B. macginitieae* uses both visual and chemosensory cues (Ache and Case 1969; Ache and Davenport 1972). Visual cues seem unlikely in the case of *B. setosus* due to the retiring habits of its host, but further investigation is needed to determine how *Pachycheles* is located and whether a shrimp is always associated with a specific host pair.

Literature Cited

Ache, B. W., and J. Case. 1969. An analysis of antennular chemoreception in two commensal shrimps of the genus *Betaeus*. Physiol. Zool., 42:361–371.

———, and D. Davenport. 1972. The sensory basis of host recognition by symbiotic shrimps, genus *Betaeus*. Biol. Bull., 143:94–111.

Butler, T. H. 1980. Shrimps of the Pacific coast of Canada. Canadian Bulletins of Fisheries and Aquatic Sciences, 202:280 pp.

Hart, J. F. L. 1964. Shrimps of the genus *Betaeus* on the Pacific coast of North America with descriptions of three new species. Proc. U.S. Nat. Mus., 115:431–466.

Karplus, I., Tsurnamal, M., and R. Szlep. 1972. Associative behavior of the fish *Cryptocentrus cryptocentrus* (Gobiidae) and the pistol shrimp *Alpheus djiboutensis* (Alpheidae) in artificial burrows. Mar. Biol., 15:95–104.

Kozloff, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. Univ. Washington Press, 226 pp.

Lassig, B. R. 1977. Communication and coexistance in a coral community. Mar. Biol. 42:85–92.

Vannini, M. 1985. A shrimp that speaks crab-ese. J. Crust. Biol., 5:160–167.

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Old Timers' Brunch opens the program on Monday, March 2; contributed paper sessions during the five-day event include sections on History and Resource Management; Birds, Fishes, and Marine Botany; Anthropology and Oceanography; Marine Invertebrates and Terrestrial Botany; Terrestrial Invertebrates and Marine Mammals; Terrestrial Vertebrates; Geology and Geography. Between sessions, you may want to examine the Channel Islands Archive at the Museum of Natural History and the Channel Islands Collections at both the Museum and the Santa Barbara Botanic Garden. These two institutions are currently the principal archival facilities in California for voucher collections and specimens which document scientific research projects and environmental studies on the islands.

Early registration is advised. In Santa Barbara, Dr. F. G. Hochberg is Program Coordinator for the event and all inquiries should be addressed to him at the Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105.

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The author should submit *at least two additional copies with the original,* on 8½ × 11 opaque, nonerasable paper, double spacing the entire manuscript. ***Do not break words at right-hand margin anywhere in the manuscript.*** Footnotes should be avoided. **Manuscripts which do not conform to the style of the BULLETIN will be returned to the author.**

An abstract summarizing in concise terms the methods, findings, and implications discussed in the paper *must* accompany a *feature article. Abstract should not exceed 100 words.*

A feature article comprises approximately five to thirty typewritten pages. Papers should usually be divided into the following sections: abstract, introduction, methods, results, discussion and conclusions, acknowledgments, literature cited, tables, figure legend page, and figures. Avoid using more than two levels of subheadings.

A research note is usually one to six typewritten pages and rarely utilizes subheadings. Consult a recent issue of the BULLETIN for the format of *notes.* Abstracts are not used for notes.

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All manuscripts should be submitted to the Technical Editor, Jon E. Keeley, Biology Department, Occidental College, 1600 Campus Road, Los Angeles, California 90041. **Evaluation of a paper** submitted to the BULLETIN begins with a critical reading by the Editor; several referees also check the paper for scientific content, originality, and clarity of presentation. Judgments as to the acceptability of the paper and suggestions for enhancing it are sent to the author at which time he or she may be requested to rework portions of the paper considering these recommendations. The paper then is resubmitted and may be re-evaluated before final acceptance. **Authors are requested to submit the names, addresses and specialities of three persons who are capable of reviewing the manuscript.**

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COVER: The kelp forest at Santa Catalina Island, California (USA) where 41 species of mollusks were associated with the kelp fronds from June 1975 through December 1976. James A. Coyer